

# LLOYDIA

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## Notes on the Linnaean Dissertations

H. W. RICKETT

(*The New York Botanical Garden, Bronx Park, New York, N. Y.*)

From 1741 Carl Linnaeus was Professor of Medicine and Botany in the University at Uppsala. In this capacity he presided over the public examinations of candidates for degrees, each of whom presented a dissertation in natural history or medicine. The dissertation was published as a pamphlet, probably on or before the day of the examination, which is given on the title-page; in the absence of evidence to the contrary we must regard this date as the actual date of publication (Int. Code Bot. Nomencl. Art. 53). That the dissertations were actually issued in this form is borne out by citations in subsequent dissertations. The title-page of one of these pamphlets is here reproduced as figure 1. At least 186 of them are known, covering a wide variety of topics in botany, zoology, and medicine. Pritzel lists 90, dated from 1743 to 1776.

The dissertations are generally attributed to Linnaeus himself, and new names published in them are ascribed to him; even though it is clear (from internal evidence) that the candidates wrote them. Just what share the professor had in the production of these works is difficult to determine. Rothmaler has argued<sup>1</sup> that, although the topics were assigned by the professor and although his influence was necessarily evident throughout the dissertations, they should be regarded as wholly the work of the students, and new names in them ascribed to these persons. The dissertations were later collected and reissued as the *Amoenitates academicae*, presumably under Linnaeus' supervision. Rothmaler would ascribe names which appear in this series for the first time (not in the original dissertations) to Linnaeus. Such distinctions seem rather far-fetched and inexpedient. Under the heading "Auctores" in the second edition of the *Species plantarum* Linnaeus listed the *Amoenitates* among his own works; and the title-pages of the volumes have "Caroli Linnaei Dissertationes." In his later works he referred to them merely by title, never citing the names of the students, though he was always careful to cite the authors of

<sup>1</sup>Repert. Sp. Nov. 49 : 272-281. 31 D 1940.

other works. Such facts imply that Linnaeus regarded the dissertations as his own work; not merely certain changes and footnotes in them. It is my understanding that, in the custom of that time, the professor furnished not only the topic but also the ideas and the data to the student; and probably names for new species. It was the student's task to substantiate the thesis and to put it into proper form for

J. C. A.  
**DEMONSTRATIONES**  
**PLANTARUM**  
 IN  
**HORTO UPSALIENSI MDCCLIII.**  
*Quas*  
*Consentiente Experient. Facult. Medica*  
*Præside,*  
*Nobilissimo & Experientissimo*  
**DN. DOCT. CAROLO**  
**LINNÆO,**  
 S:Æ R:Æ M:TIS ARCHIATRO, EQUITE,  
 Med. & Botanic. PROFESS. Reg. & Ord.  
 Acad. Imperial. N. C. Monspelienf. Stockholm.  
 Berolin. Upsalienf. Tolof. & Londin. Socio,  
 In Aud. Carol. Mai. d. III Octobr. MDCCLIII.  
*Horis ante meridiem solitis*  
*Propunit*  
**JOHANNES CHRIST. HÖJER,**  
*Uplandus.*

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UPSALIÆ,  
 Excudit LAUR. M. HÖJER, Reg. Acad. Typ.

FIG. 1. Title-page of the dissertation "Demonstrationes plantarum in Horto Upsaliensi MDCCLIII" defended in 1753 by Johannes Christian Höjer.

publication; subsequently defending it in the public examination. The names published in many dissertations other than those over which Linnaeus presided are regularly attributed to the professor. Many were defended under Carl Pehr Thunberg. The *Fasciculus observationum botanicarum* of Anders Jahan Retzius was defended by a student, as was Johann Christian Kerstens' *Primitiae florae holsaticae*.<sup>2</sup> Certainly it is more convenient to credit a large number of binomials

<sup>2</sup>The new names in this little work, however, are attributed by the author to Georg Heinrich Weber.



to "L." or to "Thunb." than to the dozens of unknown names which appear on the title-pages of the dissertations. Ascription of a name to an authority is, after all, a convention, its object being to clarify the application of the name.

The *Amoenitates academicae* form a series of ten volumes which appeared from 1749 to 1790; they contain the dissertations mentioned above with various other theses and orations. The first seven volumes were issued during Linnaeus' active years; volume 7 is dated 1769 and contains dissertations previously published, to 1768. The last three volumes were collected by Johann Christian Daniel von Schreber and published in Erlangen after the death of Linnaeus. Volume 8 contains the Linnaean dissertations from 1768 to 1776. Volume 9 includes medical dissertations from 1749 to 1775, omitted by Linnaeus from the earlier volumes. Volume 10 has further dissertations and orations of various dates by Linnaeus himself, and four by his son.<sup>3</sup>

The first seven volumes of the *Amoenitates* were reissued at Leyden or Amsterdam and finally by von Schreber at Erlangen. Some of these so-called editions are merely reprints; some contain added matter and changes in nomenclature. For the convenience of the reader the entire series is here summarized.<sup>4</sup>

#### SUMMARY OF THE EDITIONS OF LINNAEUS' AMOENITATES ACADEMICAE Vol.

1. Stockholm & Leipzig 1749. Diss. 1-18, 1743-1748.  
Leyden 1749. Diss. 1-18, not numbered or dated and in a different order from the above; the text not identical. Includes Linnaeus' "Hypothesis nova. . . ."  
Erlangen 1787.
2. Stockholm 1751. Diss. 19-30, 1749-1751; orations of 1743, 1741, 1743.  
Amsterdam 1752.  
Stockholm 1762. "aucta" according to Pritzel; not seen by HWR.  
Erlangen 1787.
3. Stockholm 1756. Diss. 31-50, 1751-1753.  
Amsterdam & Leyden 1756. Not listed by Pritzel.

<sup>3</sup>A complete table of contents of all ten volumes is given by Pulteney, *A general view of the writings of Linnaeus*, ed. 2 (1805), pp. 352-490. The contents of each are briefly abstracted.

<sup>4</sup>The desirability of knowing something of the provenance of the copy one is consulting is seen in a footnote in *Rhodora* 46: 494 (1944), which reads in part: "The bibliographic references to this plant, under *M[onarda] fistulosa*, in the recent *Review* would have gained by careful checking. The references as given there are: "*M. mollis* L., *Amoen. Acad.* 3: 390, 1764" and "*M. fistulosa* var. *mollis* L., *Sp. Pl.*, ed. 2, 2: 32, 1762." In the Stockholm (original) issue of *Amoenitates Academicæ* the description of *M. mollis* is in vol. iii. p. 399 (not 390); and, according to Pritzel, this volume was published in 1756 (not 1764). The authors thus taken to task should certainly have known that the dissertation in question appeared in the *Amoenitates* first in 1756. This critic should also have known that it was first printed in 1753. Perhaps he was aware that there was an edition of volume 3 of the *Amoenitates* in 1764; perhaps not.

- Amsterdam 1764. According to Pritzel; not seen by HWR.  
 Erlangen 1787.
4. Stockholm 1759. Diss. 51-75, 1753-1757.  
 Leyden 1760.  
 Erlangen 1788.
  5. Stockholm 1760. Diss. 76-100, 1757-1759. Classified index to the dissertations in volumes 1-5. Catalogue of publications of Laurentius Salvus.  
 Leyden 1760.  
 Erlangen 1788.
  6. Stockholm 1763. Diss. 101-124, 1759-1763. (No. 124 is dated 1759.)  
 Leyden 1764. According to Pritzel; not seen by HWR.  
 Erlangen 1789.
  7. Stockholm 1769. According to Pritzel; not seen by HWR.  
 Leyden 1769. According to Pritzel; not seen by HWR.  
 Erlangen 1789. Diss. 125-150, 1763-1768.
  8. Erlangen 1785. Diss. 151-171, 1768-1776.
  9. Erlangen 1785. Diss. 172-186, 1749-1775 (all medical). Index to the dissertations in volumes 6-9.
  10. Erlangen 1790. Diss. 1-10, including Linnaeus' "Hypothesis nova," five "Programma's", and "Oratio", "Deliciae naturae", "Disquisitio de sexu", "Pan Suecus"; and Diss. 1-4 by Linnaeus the younger.

Besides the editions shown in the summary several volumes of selections have been issued, both in the original Latin and in translation. These include a well-known volume by Benjamin Stillingfleet which appeared in 1759 and went through several editions; a collection by Leopold Bivard (1764-1766); one by F. J. Brand in 1781; and the "pars philosophica" of Jean Emmanuel Gilibert's *Systema plantarum Europae*.<sup>5</sup>

The dissertations offer valuable clues to the development of Linnaeus' thinking in several branches of botany.<sup>6</sup> In particular, many of them are important as the places of first publication of genera and species of plants; those that appeared later than the *Species plantarum* contain names which are validly published in the sense of the *International Code of Botanical Nomenclature* (1952). Complete sets are extremely rare (if any exist), and most botanists have been content to refer to the pages of the *Amoenitates*. These, however, are not identical in content with the dissertations as originally published, and their dates are not the dates of publication of the names in question.

<sup>5</sup>Stillingfleet, Benjamin. Miscellaneous tracts relating to natural history, husbandry, and physick. Translated from the Latin, with notes. i-xxx, 1-230.

Bivard, Leopold. Selectae ex Amoenitatibus Academicis Caroli Linnaei dissertationes ad universam naturalem historiam pertinentes. [I have seen only the second volume; 2: 1-297. 1766.]

Gilibert, Jean Emmanuel. Systematis plantarum Europae pars philosophica 1: 1-1xxv, i-1xxvi, 1-604. 2: 1-732, 1-52. 1786.

<sup>6</sup>This incidentally furnishes additional evidence that the substance of the dissertations was contributed by the master himself; certainly the ideas of anatomy and physiology were not original with the students.



It is obvious that collation of the two or more texts of each dissertation is necessary for an understanding of the nomenclature involved.

That at least some of the dissertations were thoroughly edited for republication in the *Amoenitates* is evident from the notes which follow. The spelling of names was sometimes "improved." Names which appeared in a dissertation were sometimes deleted in the later version; and new names were sometimes added in the latter. It is clear that the *Amoenitates* cannot be regarded simply as reprints.

#### DEMONSTRATIONES PLANTARUM IN HORTO UPSALIENSI MDCCLIII

This dissertation was publicly defended on 3 October 1753 by Johannes Christian Höjer (and printed by his brother Lorentz Magnus Höjer, printer to the Royal Academy). After the usual dedications (which are omitted in the *Amoenitates*) comes a brief introduction in which the author speaks of the value of a botanical garden to students ("cognitione enim specierum omnis solida fundatur eruditio, qua vacillante, nihil firmum est & stabile") and of the difficulty of growing in one garden plants of various climates. He goes on to notice that the Academic Garden at Uppsala now contains many plants not included in Linnaeus' *Hortus upsaliensis* of 1748, and states his intention of presenting a complete catalogue of all plants "demonstrated" (i.e., presumably, used in teaching) in 1753; his task, he says, having been made easier by the appearance of the *Species plantarum*. The names of genera and species are in fact mostly arranged in the same sequence as in this work.

The dissertation is interesting as being probably the first publication after the *Species plantarum* itself to use the Linnaean binomials; in fact the "trivial" names are here used *instead of* the full names of the species, which do not appear.<sup>7</sup> Full names (which, according to the Linnaean method, were equivalent to descriptions or diagnoses in our sense) are provided in footnotes for plants discovered so recently as not to have been included in the *Species plantarum*; but a number of the new names lack descriptions and for our purposes are "nomina nuda." Several varieties are here promoted to specific rank, but without the bibliographic references necessary, under present rules, to afford them validity. Some of these new names and combinations were maintained by Linnaeus in subsequent publications; others were not. The immediately relevant works are the *Systema naturae*, ed. 10, of 1759, and the *Species plantarum*, ed. 2, of 1762 and 1763.

We find certain names of the *Species plantarum* here used in a changed spelling; the principle of priority had not then been announced, still less the necessity of maintaining the original spelling. So *virginiana* is changed to *virginica*, and *Jasminum fruticans* is replaced by *J. fruticosum* ("Jasmiun" in the *Amoenitates*). *Ligusticum scoticum* becomes *L. scoticum*—which is the version adopted in the *Index kewensis*—and *Centaurea moschata* is changed to *C. moscata*. Other variants were doubtless due to errors on the part of one or the other of the brothers Höjer. *Ophrys myoides* (*O. insectifera*  $\alpha$  *myodes*) may be

<sup>7</sup>Trivial names, however, had been used before 1753; e.g. in the dissertation entitled *Nova plantarum genera* of 1751.

so accounted for; it is corrected in the *Amoenitates* to *O. myodes*. *Ilex agrifolium* is surely an error for *I. aquifolium*; *Ribes oxyacanthadis* for *R. oxyacanthoides*; *Cynanchum tuberosum* for *C. suberosum* and *Passiflora tuberosa* for *P. suberosa*; *Gypsophyla* for *Gypsophila*; *Euphorbia sagittalis* for *E. segetalis*; *Ranunculus sulcatus* for *R. falcatus*; *Orobis varius* for *O. vernus* (and so corrected in the *Amoenitates*); *Trifolium spinosum* for *T. spumosum* (also corrected); *Hieracium subacidum* for *H. sabaudum* (*H. subaudum* in the corrigenda, p. 27, and in the 1756 edition of the *Amoenitates*); and *Juniperus sativa* is probably *J. sabina*. The three species listed on page 12 under *Cotyledon* (Amoen. Acad. 3: 410) were presumably meant for *Sedum*. It is surprising that so many errors should appear in an academic dissertation; but the form of many of them strongly suggests that they originated in copying names from a manuscript list—perhaps the manuscript of the *Species plantarum* itself. It is even more surprising that they were not all corrected in editing the dissertation for republication.<sup>8</sup>

The following new binomials and trinomials are provided with full Linnaean names, which we can regard as descriptions, and are therefore validly published. For most of them the only new consideration adduced by this survey is the date of publication. They should be referred to this dissertation (Dem. Pl. Upsal. 1–27. 1753) rather than to the *Amoenitates* (Amoen. Acad. 3: 398–424. 1756) as they are in *Index kewensis*. They were maintained by Linnaeus in later publications except as noted.

The number before each name is that of the page of the dissertation on which it appears.

2. **Monarda mollis.** *M. fistulosa*  $\beta$  *mollis* L. Sp. Pl. ed. 2. 32. 1762. Not in Syst. Nat. ed. 10.
2. **Salvia agrestis.** *S. pratensis*  $\beta$  *agrestis* L. Sp. Pl. ed. 2. 35. 1762.
2. **Valeriana locusta discoidea.**
3. **Festuca barbata.** *F. calycina* L. Sp. Pl. ed. 2. 110. 1762.<sup>9</sup>
3. **Avena nuda.**
4. **Crucianella patula.**
5. **Cynoglossum montanum.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2.
6. **Datura ferox.**
7. **Asclepias exaltata.** *A. syriaca*  $\beta$  *exaltata* L. Sp. Pl. ed. 2. 313. 1762.
7. **Bupleurum semicompositum.**
8. **Eryngium trifidum.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2.
8. **Eryngium tricuspidatum.**
8. **Carum carvi peregrinum.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2. It is difficult to say whether *Carum peregrinum* was here

<sup>8</sup>Rothmaler suggests that Linnaeus would not have allowed in a publication of his own so many errors as appear in the original dissertation. This argument is weakened by the presence of an equal number (including some new ones) in the *Amoenitates*.

<sup>9</sup>Rothmaler refers this name to Amoen. Acad. 3: 400 (1756) "in adnot. f." I have searched in vain for such a note.



- intended, or *C. carvi peregrinum*. The text suggests the former, and it is so listed in *Index kewensis*; but the note containing the full name (description) begins "Carvi peregrinum."
11. **Zygophyllum nitraria.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2. The description is of the briefest but perhaps technically adequate. It says that this species is doubtfully placed in *Zygophyllum*, the fruit being a drupe.
  14. **Delphinium monstrosum.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2. This form is here given specific rank since it was thought to be hereditary, though monstrous.
  14. **Delphinium hybridum.** Not in Syst. Nat. ed. 10 nor in Sp. Pl. ed. 2. Only the parentage is given and the brief description "planta speciosa et glaberrima." Also "propagat speciem." The epithet seems to be intended as a true "nomen trivium" rather than as a mere descriptive epithet; its first use was in a dissertation of 1751 reprinted in 1756; the stated parentage was the same as that in the present dissertation.
  17. **Erysimum repandum.**
  18. **Malva parviflora.**
  20. **Lathyrus annuus.**
  21. **Trifolium cherleri.**
  21. **Trifolium retusum.** Lacking in Amoen. Acad., which includes, however, "Trifolium Melit. officinal.", not listed in the original dissertation. *T. retusum* is lacking also in Syst. Nat. ed. 10 and Sp. Pl. ed. 2.
  24. **Micropus erectus.** Although this name was previously and validly published in the *Species plantarum* (in Addenda, after the Indexes), it is here provided with a fuller description and citations.
  26. **Bryonia punctata.** *Trichosanthes punctata* L. Amoen. Acad. 3: 421. 1756. This appears also in Sp. Pl. ed. 2. 1432, but as "genere dubia, cum non floruerit"; not in Syst. Nat. ed. 10 under either genus.

## HERBARIUM AMBOINENSE

This is the earliest of several attempts to identify and name the species of Georg Everard Rumphius' great work of the same name, edited by Johannes Burman and published from 1741 to 1755. The dissertation is by Olaf Stickman and is dated 11 May 1754.

The lineal descendant of this opusculum is the monumental volume by Elmer Drew Merrill.<sup>10</sup> Merrill writes of Stickman's dissertation as "being probably the first work published following the binomial system of nomenclature after the system was proposed" (p. 31). Reference to my notes on the *Demonstrationes* above makes it clear that this is not so; and, in fact, there is considerable question whether Stickman can be said to have used the "binomial system," for many of the new names are "polynomials." Under Art. 79 of the present code, specific names must be rejected if they appear in works in which binomials were not "consistently" employed; Merrill's work antedated the

<sup>10</sup>An interpretation of Rumphius's *Herbarium amboinense*. Bur. Sci. Manila Publ. 9: 1-595. 2 maps. 1 N 1917.

adoption of this rule in 1930. There is a note, however, in the *Code* to the effect that Linnaeus is considered to have used binomials from 1753 on, in spite of certain exceptions. If this principle can be applied to this dissertation, then Merrill is perhaps justified in picking up the first adjective of the full name and treating it as a specific epithet, although it is not distinguished typographically or in any other way from the rest of the name (e.g. *Hernandia ovigera, foliis ovatis basi petiolatis* is taken as publication of *Hernandia ovigera* L.). That Linnaeus himself may have regarded the first qualifying word as the "trivial name" is indicated by the thesis entitled *Centuria I. plantarum* (see below), in which some of the species named in Stickman's dissertation are so listed; similarly Linnaeus, in editing the dissertation for republication in the *Amoenitates*, shortened some (not all) of the specific names to trivial names for the second edition. The rule obviously needs clarification with such cases in mind.

In any case, since most of the names defended by Stickman were taken up in the subsequent editions of the *Systema naturae* and/or the *Species plantarum*, which shortly followed their appearance in the pamphlet, no nomenclatural trouble would seem to result from rejecting them in the latter place; it is merely a question of correct citation. I do not know which came out first, the fourth volume of the *Amoenitates* or the tenth edition of the *Systema*. Merrill lists the former in first place (except for *Excoecaria agallocha* and *Sesuvium portulacastrum*, where the order is reversed; and *Lagerstroemia chinensis*, which he rejects in favor of *L. indica* on the basis of general acceptance of the latter).

Stickman in his introduction writes of the difficulty of obtaining specimens from "India" and the scarcity of botanists willing to undertake such difficult and dangerous journeys. This leads to a brief encomium of the "peregrinatores"—Hermann, Sloane, Banister, Kaempfer, Plumier, Rheedé, Rumphius; and of the "more recent" explorers, Feville, Kalm, Hasselquist, Osbeck, Mylius, Adanson, Löfling. He gives a very brief sketch of the division of India into "Old India" and "India aquosa." This is followed by a sketch of the life of Rumphius, and brief mention of Burman who brought out the *Herbarium amboinense* after Rumphius' death. Herein is the principal difference between the original dissertation and the revised version (*Amoen. Acad.* 4: 112–143); for when the former was written only six volumes of Rumphius' work had appeared, but the seventh is included in the second version of the dissertation, and the wording of the introduction is accordingly modified.

Most of the *Species plantarum*, according to Stickman, had been written before Linnaeus saw Rumphius' work; Stickman's task was therefore to identify Rumphius' plants with Linnaeus' species and place Rumphius' names in the synonymy of those of Linnaeus. Because of Merrill's work it is unnecessary here to list the solutions proposed in the dissertation. The new "binomials" made in both original and later editions are shown by Merrill (p. 33, 34), as they were by Juslenius in the first *Centuria*. Both lists are incomplete; and the list below may well be also. I have found 37 new names in all, 25 in the original thesis of which one was omitted in the *Amoenitates*; 12 additional in the



latter, of which one was merely a new combination. All but 16 appear in the tenth edition of the *Systema*; more are lacking from the second edition of the *Species plantarum*. Pertinent synonymy is shown by Merrill and need not be here repeated.<sup>11</sup>

The number which precedes each name is that of the page of the dissertation on which it appears. Names lacking in the original dissertation but added in the *Amoenitates* are enclosed in brackets.

- |                                     |                                         |
|-------------------------------------|-----------------------------------------|
| 7. <i>Garcinia celebica</i> .       | 21. <i>Bromelia comosa</i> .            |
| 7. <i>Psidium cujavus</i> .         | 23. <i>Dolichus tetragonolobus</i> .    |
| 9. <i>Laurus culitlawan</i> .       | [ <i>Phaseolus cylindricus</i> .]       |
| 9. <i>Myrtus leucadendra</i> .      | 23. <i>Dolichus pruriens</i> .          |
| [ <i>Excoecaria agallocha</i> .]    | 24. <i>Momordica indica</i> .           |
| 10. <i>Erythrina variegata</i> .    | 24. <i>Momordica trifolia</i> .         |
| 13. <i>Rhizophora caseolaris</i> .  | 24. <i>Plumbago indica</i> .            |
| 13. <i>Rhizophora corniculata</i> . | 25. <i>Pothos latifolius</i> .          |
| 14. <i>Ricinus mappa</i> .          | [ <i>Eriocaulon setaceum</i> .]         |
| 14. <i>Adenanthera falcata</i> .    | [ <i>Panicum vulpinum</i> .]            |
| [ <i>Muntingia bartramia</i> .]     | [ <i>Justicia bivalvis</i> .]           |
| 14. <i>Ricinus tanarius</i> .       | 27. <i>Ophioglossum pendulum</i> .      |
| 14. <i>Hernandia ovigera</i> .      | 28. <i>Pancratium narbonense</i> .      |
| 16. <i>Convallaria fruticosa</i> .  | [ <i>Sesuvium portulacastrum</i> .]     |
| 18. <i>Lens phaseoloides</i> .      | [ <i>Phyllanthus epiphyllanthus</i> .]  |
| 18. <i>Tragia scandens</i> .        | [ <i>Varneria augusta</i> .]            |
| 18. <i>Menispermum flavum</i> .     | [ <i>Lagerstroemia chinensis</i> .]     |
| 19. <i>Piper decumanum</i> .        | [ <i>Casuarina equise (ti) folia</i> .] |
|                                     | [ <i>Canarium indicum</i> .]            |

#### CENTURIA I. PLANTARUM

This was presented on 19 February 1755 by Abraham D. Juslenius. It contains names, descriptions and synonyms (on the model of the *Species plantarum*) of 101 plants picked at random from among those newly discovered and sent to Linnaeus. The brief introduction is confined to generalities; it mentions the explorations of Kalm, Löffling, Osbeck, Hasselquist, Sauvages, Aymen, Monnier. As an example of the progress of botany since 1753 a list is included (incomplete) of the new species named in the *Demonstrationes plantarum* and the *Herbarium amboinense*.

Of the species named, over one-fifth came from Spain, doubtless as a result of Löffling's collecting. (Juslenius mentions the collectors of some, but not all, of the species.) Other parts of Europe accounted for another third of the century. Arabia is represented by 10 numbers and Egypt by the same number; Hasselquist's name of course appears with some of these. Other regions mentioned are Palestine, Aethiopia, Lusitania, the Cape of Good Hope, China, India, North and South America, the West Indies.

The names are provided with epithets (trivial names) in parentheses and italic. Those published in the original pamphlet should be cited with the date 1755 rather than 1759, the date of the corresponding part of the *Amoenitates* (4: 263-296).<sup>12</sup> With few exceptions the names

<sup>11</sup>In *Index kewensis* these names are variously referred to Syst. Nat. ed. 10, to Sp. Pl. ed. 2, to Amoen. Acad. 4, and to the dissertation itself.

<sup>12</sup>The abbreviation "Cent. I." is suggested; not "Cent. Pl. Rar. i" as *Index kewensis* has for some species.

appear in the tenth edition of the *Systema* and the second edition of the *Species plantarum*.

The following names pose various problems of correct citation. The number which precedes each is that of the page of the dissertation on which it appears.

7. **Mirabilis longiflora.** This is ascribed in *Index kewensis* to Svensk. Vet.-Akad. Handl. 1755: 176. I have no information on the question of priority of this over the dissertation.
11. **Saxifraga ajugaefolia.** The epithet is changed to *ajugifolia* in Amoen. Acad. 4:271. Those who hold to a strict interpretation of the *Code* will prefer the earlier version.
11. **Dianthus hyssopifolius.** In the *Amoenitates* the name is changed to *D. superbus*. The cited synonyms are different, but it seems clear that the same species is meant, as may be seen from the detailed description; this, though modified, emphasizes the same characters. The earlier name was abandoned also in Linnaeus' later works.
13. **Potentilla heptaphylla.** This becomes *P. opaca* in the *Amoenitates* and later works. The description is modified apparently by the discovery that the radical leaves were "quinatis" instead of "septenatis"; and the trivial name, of course, had to be changed in consequence. If the species is maintained, the earlier name must be used; and joins the company of such unfortunate names as *Asclepias syriaca*, bestowed under a misapprehension. Priority has its drawbacks.
14. **Cistus hirta.** This is omitted in the *Amoenitates*; and the numbering of the species in the two versions is different from this point on. There is a *C. hirtus* L. Sp. Pl. 528 (1753), but this is a different species.
16. **Antirrhinum molle.** The name is changed in the *Amoenitates* to *A. glaucum*; doubtless because of the existence of *A. molle* L. Sp. Pl. 1198 (1753). The epithet *molle* must have been given to the plant of this century as a result of some sort of error or confusion, since this is described as having "caules . . . uti tota planta glauco-virides"; the epithet *glaucum* obviously corrects the error. *A. glaucum* in this sense is maintained in later works. *A. molle* appears also in Dem. Pl. Upsal. 16 (1753), but since it is not there provided with a description it is impossible to say in which sense it was meant.
17. **Antirrhinum spartum.** Of this name the *Index kewensis* says "postea *sparteum*." But *A. sparteum* L. Sp. Pl. 1197 (1753) is evidently, from the description and citations, another species; which is probably what moved the editor of the *Amoenitates* to change *A. spartum* to *A. junceum*. The two species are maintained in Syst. Nat. ed. 10. 1111, 1112 and Sp. Pl. ed. 2. 854, 856; but in the latter work Linnaeus himself compounds the confusion by citing Amoen. Acad. 4: 277 for both. *A. spartum* appears also in Dem. Pl. Upsal. 16 (1753), but as a name only.
17. **Iberis badensis.** This is lacking from the *Amoenitates* and from Linnaeus' later works. To judge from the citations it is synony-



mous with *Thlaspi montanum* L. Sp. Pl. 647 (1753); the description of which was considerably amplified in the second edition (p. 902).

[*Geranium scabrum* is inserted in the *Amoenitates* (4:281); it is not in the original dissertation.]

21. **Geranium versicolor.** For this is substituted the name *G. striatum* in the *Amoenitates*, with a modified and amplified description. This apparently superfluous name is maintained in the later works.
23. **Lupinus stoloniferus.** The name is lacking from the *Amoenitates* and from the later works. Even the number corresponding to this species is omitted in the later version; there is no 64 in the dissertation as republished in the *Amoenitates*.
24. **Trifolium uniflorum.** Reference is made ("Confer.") to *T. uniflorum* L. Sp. Pl. 771 (1753); the author was evidently in some doubt whether or not he had the same species. The description he gives and the synonyms cited are different.  
Nothing better illustrates that to the botanists of the 18th century the trivial name was relatively unimportant; the essential thing was the "polynomial." The trivial name derived its sanction more from propriety than from priority (compare *Potentilla heptaphylla*, above).
24. **Trifolium cherleri.** This was published in Dem. Pl. Upsal. 21 (1753), and is here republished with a much fuller description. Note that *both* the dissertations antedate the republication of the first in the *Amoenitates*.
26. **Hieracium tomentosum.** In the *Amoenitates* this is transferred to *Andryala* as *A. lanata*; which name is maintained in Linnaeus' later works.
29. **Coreopsis leucanthema.** The spelling is changed to *leucantha* in Sp. Pl. ed. 2. 1282; this is the version adopted in *Index kewensis*.
33. **Valantia cucullaris.** This is the original spelling, whether or not it may be regarded as erroneous. In all other places it appears as *V. cucullaria*.

#### CENTURIA II. PLANTARUM

This was defended on 2 June 1756 by Eric Torner; it is a continuation of the preceding. After the usual rather flowery exordium on the new dispensation in botany, Torner mentions the sources of his plants: many were collected near Verona by Seguer, near Montpellier by Sauvages, at the Cape of Good Hope by Burman; some came from Philip Miller's garden at Chelsea. Nearly half were from Europe (of which 12 from Italy); 21 were from India; 14 from Ethiopia; 6 from South America; and the remainder from Egypt, Syria, Mexico, Carolina, Virginia, China and Ceylon.

The names are numbered consecutively with those of the first century; that is, they begin with no. 101. But if the original pamphlets are compared, there are two species numbered 101, for there were 101 species in the first. In revising the latter for republication there were deletions and additions, and the number 64 was entirely omitted; so that only 99 species are actually to be found in the version published

in the *Amoenitates* though the numbers run to 100. Since the second *Centuria* was originally issued three years *before* the revised version of the first, the author may have had a corrected version of the latter before him. In the *Amoenitates*, moreover, the second *Ceniuria* is placed out of chronological sequence, in order, doubtless, to bring it next to the first.

With a few exceptions the names of the species here described appear also in the tenth edition of the *Systema* and the second edition of the *Species plantarum*. The *Systema* and the fourth volume of the *Amoenitates* must have been published very nearly together. It may be noticed that citations in the *Systema* are to the *Centuria* (i.e., to the original dissertation), while those in the *Species plantarum* are to the *Amoenitates*. The following names merit attention. The number which precedes each is that of the page of the dissertation on which it appears.

4. ***Ixia plicata***. This is lacking in the later editions of *Systema* and *Species plantarum*.
9. ***Lysimachia monnieri***. In the *Amoenitates* this is transferred to *Gratiola* as *G. monnieri*.
11. ***Diosma crenulata***. In his later works Linnaeus' used the spelling *crenata*.
12. ***Nerium zeylonicum***. In the tenth edition of the *Systema* this is changed to *N. zeylanicum*; *Index kewensis* adopts the later spelling.
13. ***Gomphrena brasiliana***. Cited in the *Systema* as *G. brasilien[is]*.  
[*Dianthus monspessulanus* was first published in the *Amoenitates*; it is not in the original dissertation.]
20. ***Betonica hirta***. This is lacking in the *Amoenitates*; the numbers in the two versions correspond from this point, since this deletion compensates for the above insertion. *Betonica hirta* is lacking also in Sp. Pl. ed. 2.
23. ***Acanthus dioscoridis***. This is lacking in the *Systema*.
27. ***Malva scabrosa***. *M. capensis*  $\gamma$  *scabrosa* of later works.
27. ***Anthyllis lotoides***. This was changed in the *Amoenitates* to *A. asphaltoides*, doubtless because of the existence of *A. lotoides* L. Sp. Pl. 720 (1753). In Syst. Nat. ed. 10. 1160 (1759) the epithet is spelled *aspalatoides*. The word *asphaltoides* is of dubious application, but the fitness of *aspalatoides* is seen in its later transfer by Linnaeus to the genus *Aspalathus* (*A. anthylloides* L. Sp. Pl. ed. 2. 1002. 1763). *Asphaltoides* may therefore be an error and *aspalatoides* a correction. It was further changed to *aspalathoides*. If this is accepted, the correct name for the species is (unfortunately) ***Aspalathus aspalat[h]oides***.
29. ***Lactuca serriola***. In the second edition of the *Species plantarum* this is changed to *L. scariola*; and this name has been almost universally adopted. The two epithets seem not to be orthographic variants of the same word; both were known to B  uhin and others being used for various Compositae; they seem to have been derived from the Arabic. If this is so, then the earlier version must be maintained.
30. ***Bidens atripicifolia***. An obvious mis-spelling, to be corrected.
31. ***Anthemis fruticosa***. Omitted from the later works.



## The Structure and Development of the Caryopsis in Some Indian Millets

### III. *Panicum miliare* Lamk. and *P. miliaceum* Linn.

S. NARAYANASWAMI

(*The University of Michigan, Ann Arbor, Mich.*)

This part of the series deals with the embryology of two species of *Panicum*, namely *Panicum miliare* Lamk., called the Little Millet, and *Panicum miliaceum* Linn., the Proso-millet or Broom corn, both belonging to the tribe Paniceae. The earliest reference to the genus is contained in the works of Hofmeister (1861), Westermaier (1890), Kennedy (1900) and Suessenguth (1919). Recently Khosla (1946) has made a few comparative observations on the embryology of four Indian millets of which *Panicum miliaceum* is one. Investigations on the plants were made in order to elucidate detailed information on the developmental morphology of the grain namely, megasporogenesis, the method of embryo formation, the fate of the integuments and the nucellus, the persistence or otherwise of the antipodal cells, endosperm formation and the concomitant changes in the wall layers of the pericarp. The study also included a consideration of the method of pollen formation.

*Material and methods.*—The plants under investigation were grown at the University Botanical Garden, Delhi, from seeds supplied by the Millet Specialist, Coimbatore, India. Young spikelets were fixed on the spot as such in formalin acetic alcohol while for older spikelets, the glumes were clipped off in order to facilitate penetration. For the study of embryo and kernel development, the maturing endosperm was punctured on the surface or the top portion sliced off to ensure complete infiltration of paraffin. Dehydration and imbedding were done in the usual way using xylene as clearing agent. Sections were cut at 10–18  $\mu$  depending on the stage of development. Safranin and fast green combination gave better results than Haidenhain's haematoxylin.

#### panicum miliare Lamk.

*Floral organs.*—The inflorescence is a panicle consisting of a number of racemes. The spikelets are solitary or in pairs. Each has a short slender axis, the rachilla, bearing two florets subtended by a pair of empty glumes, the lower almost enveloping the upper. The lower floret is staminate and comprises the lemma, palea, and the three stamens while the upper floret is perfect and provided with a lemma, palea, two lodicules, three stamens, and a smooth spherical unilocular ovary with two long styles bearing plumose stigmas. Fig. 1 represents a longitudinal section of the spikelet and Figs. 2–4 show its various parts.

The rachilla, as seen in transverse sections, has a central vascular bundle with two smaller peripheral ones surrounded by a common sclerenchymatous bundle-sheath (Fig. 2, *scl. sh*). The cortex is 3–4 layered. The innermost layer of the cortex consists of conspicuously enlarged rounded parenchyma cells. This forms the chlorophyll-





Meiosis is normal and of the successive type (Figs. 7, 8). The pollen tetrads show the tetrahedral or the isobilateral arrangement. The exine is smooth and possesses a single germ pore.

With progressive differentiation of the wall of the anther the microspores enlarge and commence to form the male gametophyte. The stages leading to the formation of the tube and generative cells follow the normal course (Figs. 9, 10). The pollen grains are three-celled at shedding (Fig. 11). The vegetative nucleus is always found in an advanced state of degeneration. Supernumerary nuclei arising from the division of either the vegetative or the generative nucleus are not infrequent (Figs. 13, 14).

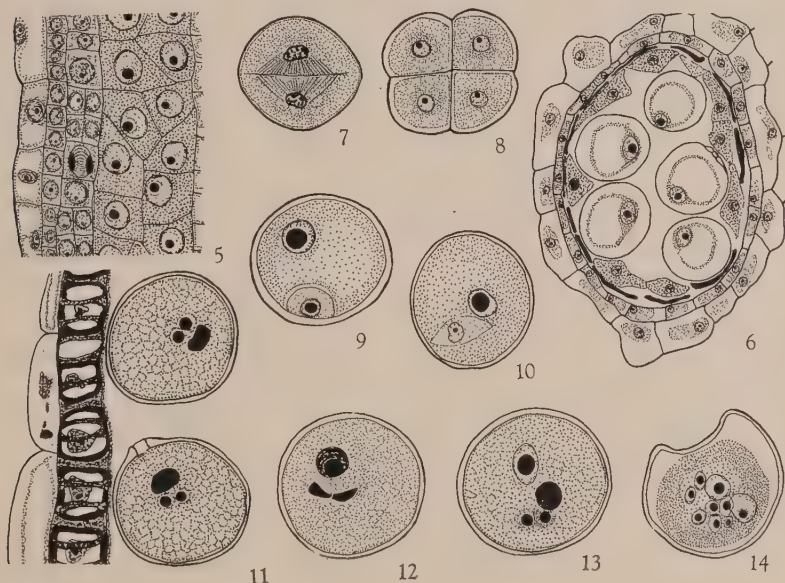


PLATE 2.—FIGS. 5-14.—Microsporogenesis and male gametophyte. FIG. 5. L. s. portion of anther wall showing epidermis, endothecium, middle layer, tapetum and pollen mother cells.  $\times 86$ . FIG. 6. C. s. anther lobe: note degenerated remnants of middle layer and uninucleate tapetal cells.  $\times 86$ . FIG. 7. Meiosis I in pollen mother cell.  $\times 167$ . FIG. 8. Pollen tetrad.  $\times 167$ . FIGS. 9, 10. Pollen grains showing tube and generative cells.  $\times 167$ . FIG. 11. Portion of anther wall and pollen grains at maturity.  $\times 167$ . FIG. 12. Three-celled pollen grain.  $\times 167$ . FIGS. 13, 14. Pollen grains showing supernumerary nuclei.  $\times 167$ .

*Megasporogenesis and embryo sac formation.*—The hypodermal archesporial cell differentiates as the topmost of a row of nucellar cells (Fig. 15). No parietal cell is cut off and the cell itself becomes the megaspore mother cell (Fig. 16). The nucellar epidermis frequently becomes two-layered by a periclinal division. The two integuments begin to differentiate at this stage. The inner one forms the micropyle while the outer does not grow beyond a third of the periphery of the nucellus.

Meiosis in the megaspore mother cell is normal. Division I (Fig. 17) results in the formation of the dyad cells of which the upper may

be slightly smaller than the lower. Fig. 18 shows metaphase of Meiosis II in both dyad cells but usually there is no such synchronization and the division in the chalazal dyad cell precedes that in the micropylar. Fig. 19 shows the nucleus of the upper dyad cell in resting condition and that of the lower, in metaphase. In Fig. 20 the upper is in metaphase and the lower in telophase. Or, the homotypic division in the lower dyad cell is already completed while the upper just starts to divide (Fig. 21). However, division in the upper dyad cell seldom proceeds to completion before the cell starts to degenerate (Fig. 22). When it does, an oblique wall is laid down.

A linear tetrad of megaspores or a triad row of three cells (Fig. 23) is formed. The micropylar ones, as usual, degenerate and the chalazal one becomes the embryo sac mother cell. The degenerated megaspores persist for a time as darkly stained elongated streaks with a flattened top abutting the nucellar epidermis (Fig. 24). The functional megaspore undergoes progressive enlargement and by three successive divisions, an octonucleate 7-celled female gametophyte is formed (Figs. 25-28). The polar nuclei lie close to the egg cell, embedded in dense cytoplasm. The egg cell is pear-shaped and has a narrow basal attachment (Fig. 29). It protrudes slightly beyond the level of the synergids. The latter are pyriform and show no basal vacuoles. They may develop hooks but the longitudinal striations characteristic of the filiform apparatus are not very pronounced. They, however, commence to degenerate prior to fertilization.

The three primary antipodal cells form a triangular group and do not divide. The cells remain uninucleate throughout development. Two types of antipodals are characteristic of the species. In some ovules they appear elongated with pointed ends penetrating into the surrounding nucellar tissue (Figs. 30, 31). Or, they appear considerably swollen showing prominent nuclei and dense cytoplasm. Frequently the cells degenerate before fertilization. A longitudinal section of the ovary at this stage is shown in Fig. 32.

*Fertilization and embryogeny.*—The pollen tube passes between the outer integument and the ovary wall. It penetrates the micropyle and enters the embryo sac. The tip of the tube reaches the base of the egg and discharges a crescent of X-bodies which is a characteristic accompaniment of a stage showing fertilization. Though the actual fusion of the male nuclei with the egg and the polar nuclei was not observed, it is presumed to follow the usual course described for the rest of the Paniceae investigated by me. The zygote undergoes a short period of rest while the primary endosperm nucleus starts to divide soon after formation.

The first wall is transverse so as to divide the zygote into equal halves *a* and *b* (Fig. 33). A second division, also transverse, occurs in the basal cell to give rise to the two cells *c* and *d*, while the division in the terminal cell is vertical and parallel to the long axis of the ovule. This results in a 4-celled proembryo (Fig. 34), formed at a time when the embryo sac has 20-25 free endosperm nuclei. The next division is vertical in the cell *c* and in the terminal tier *a* but at right angles to the previous division in the latter. As a result, the terminal tier forms a quadrant (Fig. 35) and the proembryo becomes 7-celled. Often





PLATE 3.—(*col*, coleoptile; *i.i*, inner integument; *nu*, nucellus; *o. i*, outer integument; *s. m*, stem meristem; *sty*, style). FIG. 15, L. s. young ovule showing hypodermal archesporial cell. x 80. FIG. 16, Same, showing megaspore mother cell in diakinesis. x 80. FIG. 17, Telophase I in m.m.c. x 80. FIGS. 18-21, dyad cells showing Meiosis II. x 160. FIGS. 22, 23, Linear row of three megaspores. x 160. FIG. 24, L. s. ovule showing functional megaspore. x 80. FIGS. 25-27, Two-nucleate and four-nucleate embryo sacs. x 80. FIG. 28, Young organized embryo sac. x 80. FIG. 29, Micropylar portion of embryo sac. x 160. FIG. 32, L. s. ovary at pollination. x 35. FIG. 35, Embryo sac showing bi-celled proembryo, free nuclear endosperm and glandular antipodal cells. x 160. FIGS. 34-39, Stages in development of embryo. FIGS. 34-37, x 160; FIGS. 38, 39, x 35.

oblique vertical divisions occur in the terminal tier (Figs. 36, 37). The basal cell *d* divides transversely so as to cut off the suspensor initial *f* which undergoes a series of transverse divisions to form the tiers *g*, *i* and *j* (Fig. 37), followed by vertical ones so that a somewhat massive multicellular suspensor 2-3 cells wide and 5-6 cells high, is formed (Fig. 38). Vertical divisions follow in the tiers *e* and *c* contributing to the formation of the proembryo which appears spherical (Fig. 39). A longitudinal section of the ovary at this stage is shown in Fig. 40. The remnants of the pollen tube and the synergids persist when the proembryo is 4-7 celled (Fig. 41, *pt*, *syn*).

This sequence of cell division in the fertilized egg appears to be fairly constant. The terminal tiers show active cell division but this is not so in the suspensor region. In later stages of growth the original cell boundaries are no longer perceptible so that it was not possible to identify the regions that originated from any of the sectors of the proembryo. A feature, common with the rest of the Gramineae, during embryogenesis is the propensity of the endosperm nucleus to divide soon after triple fusion while the zygote undergoes a period of rest (Figs. 42, 43).

The proembryo is clubshaped before any external differentiation can be perceived. A slight indentation on the front face below the apex of the growing embryo is the first visible sign of the formation of the growing point (Fig. 44). Fig. 44 shows a longitudinal section of the micropylar portion of the ovule at this stage. The primordia of the coleoptile and the primary leaves (Fig. 45) are laid down as reported for other grasses. The cells of the epithelium in contact with the endosperm are more or less squarish. Fig. 46 represents a vertical section of a mature embryo.

It lies on one side at the base of the caryopsis. It comprises the radicle ensheathed by the parenchymatous tissue of the coleorhiza and the terminal plumule enclosed by the coleoptile, connected by a short axis and attached to the scutellum which almost envelops the various organs. The scutellum extends upwards beyond the coleoptile and runs further down to the level of the radicle, separated by a cleft. A short ligular process is seen over the upper portion of the scutellum above the coleoptile. Except for the procambial strands consisting of elongated thin-walled cells, no mature elements are differentiated in the embryo. The primary root appears to be polyarch with 7-8 groups of protoxylem initials (*px*) distributed around the central metaxylem vessels (*mx*) of wider lumen (Fig. 47). At the nodal region where the coleoptile originates, the vessels tend to run obliquely outwards. A cross section at the nodal region reveals the method of distribution of the procambial strands to the differentiating organs. In the center is the nodal plexus or the transaxis plate consisting of obliquely running procambial elements. Above this, the strand forms two groups separated by metaxylem elements of larger caliber (Fig. 48).

The larger of the two groups runs obliquely outwards toward the scutellum and assumes the shape of a horse-shoe. The other group forms the median trace (*m.tr*). The horse-shoe shaped structure is then broken up into three strands, the middle one extending to the



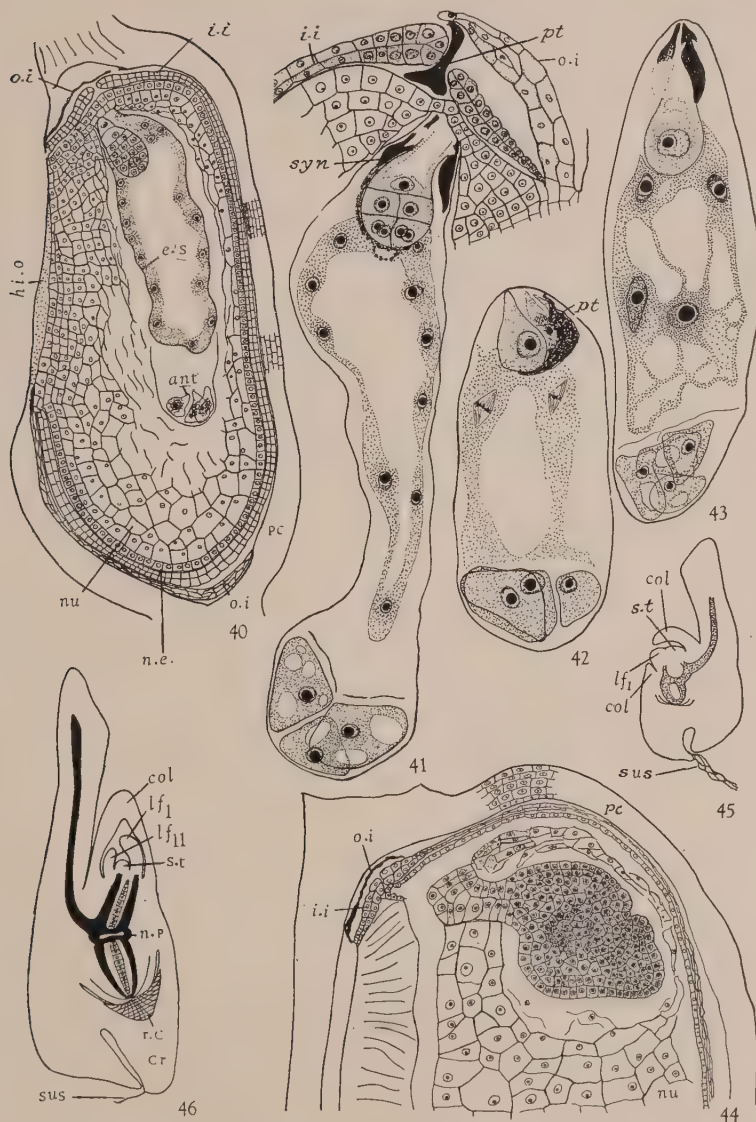


PLATE 4.—(*ant*, antipodals; *col*, coleoptile; *cr*, coleorhiza; *e.s.* embryo sac; *hi.or.* hilar orifice; *i.i.* inner integument; *lf<sub>1</sub>* and *lf<sub>2</sub>*, primary leaves; *n.p.* nodal plate; *n.e.* nucellar epidermis; *nu*, nucellus; *o.i.* outer integument; *pc*, pericarp; *pt*, pollen tube; *rc*, root cap; *sus*, suspensor; *syn*, synergids). FIG. 40. L. s. ovary at free nuclear stage of endosperm. x 36. FIG. 41. Micropylar portion of ovule and embryo sac. x 80. FIG. 42. Embryo sac showing zygote, remnants of pollen tube and division of endosperm nuclei. x 80. FIG. 43. Zygote surrounded by endosperm nuclei. x 35. FIG. 44. Micropylar portion of young caryopsis; the outer integument is degenerated and proembryo has commenced to differentiate. x 35. FIGS. 45, 46. L. s. differentiating and mature embryos. x 16.

scutellum forms the scutellum trace (Fig. 49). The other two deflect upwards supplying a trace each to the two sides of the coleoptile (Fig. 50, *col. tr*). At the base of the coleoptile node the median trace breaks up into several strands running parallel outwards forming the median bundle and a number of smaller bundles for the first foliage leaf. No primordia of secondary roots or an epiblast are present. Figs. 50 and 51 show the scutellum (*sc*) partially surrounding the coleoptile (*col*), the primary leaf (*pr. 1*), and the stem tip (*s.t.*), and Fig. 51a represents a cross section above the stem apex showing the imbricate nature of the primary leaf within the coleoptile.

*Endosperm*.—The two nuclei formed by the division of the primary endosperm nucleus divide simultaneously (Fig. 42). Of the four nuclei thus formed, two migrate to the lower end of the embryo sac and the other two remain near the micropylar portion (Fig. 43). A large number of free nuclei is formed by a series of successive divisions. Approximately 16 free nuclei are formed when the zygote divides. The cellular phase of the endosperm begins in the region around the proembryo and then at the antipodal region extending from the periphery towards the center. The tissue in contact with the embryo appears more or less flattened consisting of cells of smaller caliber but in the antipodal region, the cells are polygonal and larger in size.

In later stages of growth, cell division is confined to the peripheral zone, except in the basal and crown regions of the endosperm. A few periclinal divisions, first of the epidermal layer and later of the underlying layers, produce radially arranged rows of cells (Fig. 54). When the meristematic activity ceases, the surface layer of the endosperm functions as the aleurone layer.

Starch grains get deposited in the endosperm cells. The nuclei which were at first active and showed prominent nucleoli gradually disorganize and in the mature kernel, only their crushed remnants are seen.

*Fruit and seed*. (a) *Pericarp*. The ovary wall consists of 4–5 cell layers. The outer epidermal cells are rectangular with their long diameters parallel to the length of the caryopsis, while those of the inner epidermis are narrow, elongated and tubular. The two hypodermal layers consist of cells that are uniformly thin-walled and rectangular, while the layer adjacent to the inner epidermis consists of cells that are more or less square. As the caryopsis matures, the cell layers become greatly stretched, leaving large intercellular spaces between the cells of the mesocarp. Later the middle layers are disorganized and completely resorbed, leaving only the two epidermal layers firmly pressed against each other in the mature caryopsis (Fig. 55). Fig. 56 represents a surface view of the epidermal layers of the mature pericarp.

(b) *Testa*.—The two integuments consist of thin-walled parenchyma. The inner one is typically two-layered and forms the micropyle (Figs. 40, 41) while the outer one is 2 or more layered at the integument-insertion region and 6–8 layered at the stylar canal region. The latter does not extend beyond a third of the periphery of the nucellus. It may protrude into the stylar canal and cap over in the region of the micropyle. Signs of degeneration are noticed in the outer in-



tegument when the proembryo is but three-celled. The cells appear elongated showing scanty cytoplasm and disintegrating nuclei, the outer walls of the cells becoming somewhat wavy and irregular. The degeneration becomes more pronounced as embryo development proceeds. The portion of the integument at the styler end disorganizes

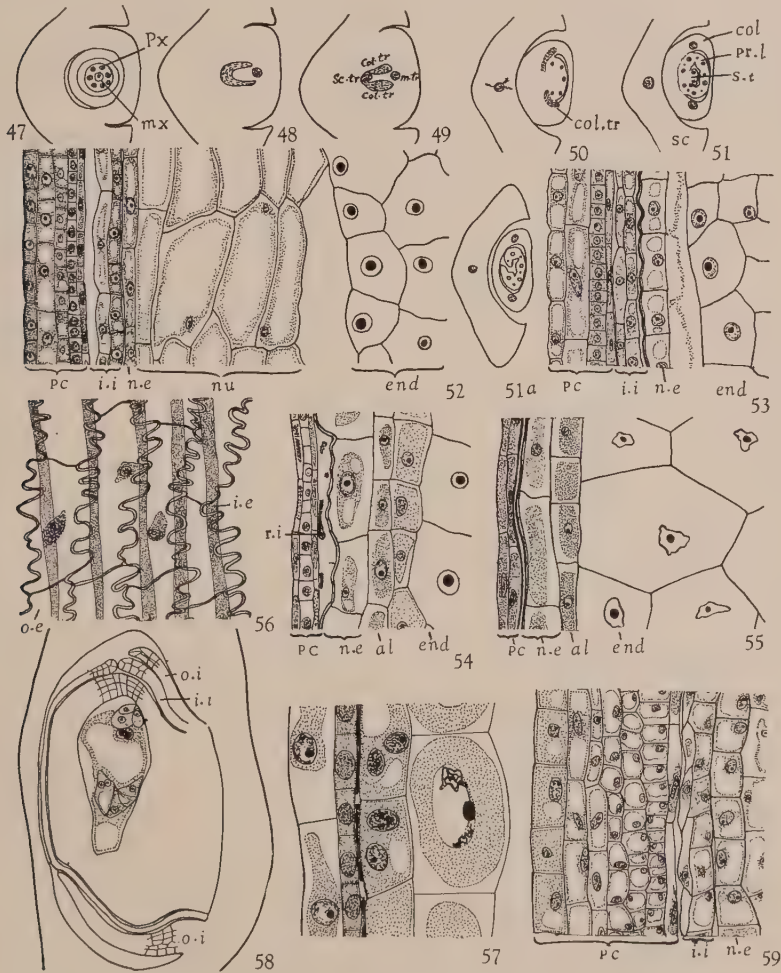


PLATE 5.—(*al*, aleurone layer; *col.tr*, coleoptile trace; *end*, endosperm; *mx*, metaxylem; *m.tr*, median trace; *px*, protoxylem; *pr.l*, primary leaf; *r.i*, remnants of inner integuments; *sc*, scutellum; *Sc.tr*, scutellum trace; *s.t*, stem tip. Others as in previous plate). FIGS. 47-51a. C.s. mature embryo to show distribution of vascular strands. x 16. FIGS. 52-55. L.s. peripheral portions of caryopsis at different stages of growth. x 80. FIG. 56. Surface view of outer and inner epidermal layers of pericarp. x 80. FIG. 57. L.s. portion of young anther. x 164. FIG. 58. L.s. ovule at pollination. x 40. FIG. 59. L.s. peripheral portion of young ovary. x 84.

earlier than that over the micropylar end when the proembryo is about 15–20 cells. In the mature stage all that remains of the outer integument is but a wavy thread-like structure persisting for a while, before final obliteration (Figs. 40, 44).

The outer layer of the inner integument disorganizes, first at the sides of the ovule and then in the region close to the base of the style. When the disorganization of this layer is well advanced, that of the inner layer commences. Scanty remnants of cytoplasm and isolated nuclei are observed between the suberized nucellar epidermis and the pericarp, when the disruption is fairly complete. In the mature caryopsis, however, even these are resorbed leaving no remnants. Figs. 52–55 show peripheral portions of the ovule at different stages of growth.

(c) *Nucellus*.—In the region of the micropyle, the nucellus may become double-layered. During development of the endosperm much of the nucellar tissue is consumed. The nucellar epidermis alone, becomes conspicuous owing to suberization of the outer tangential walls of the cells (Figs. 53, 54). In the fully mature caryopsis, it may form a persistent layer interposed between the pericarp and the aleurone over the entire surface (Figs. 40 and 55) except over the germinal face of the proembryo, although the cells composing the layer are in a state of collapse.

#### panicum miliaceum Linn.

Investigations on another species of *Panicum*, namely, *P. miliaceum*, were undertaken for comparison, especially as Khosla's (1946) work did not seem fully dependable. The main features are as follows.

Meiosis in pollen mother cells is normal. The anther wall consists of the usual number of cell layers of which only the epidermis and endothecium persist. The tapetum differs from that of *P. miliare* in that the cells are binucleate (Fig. 57) instead of being uninucleate as in the latter. The pollen grains are three-celled at shedding.

The ovule is invested by two integuments of which the inner alone takes part in the formation of the micropyle. Meiosis in the hypodermal megaspore mother cell is normal but the second meiotic division in the micropylar dyad cell may not proceed to completion before it starts to degenerate. This results in the formation of a row of three cells. If the division is completed, usually a T-shaped tetrad is formed.

The embryo sac develops essentially like that of *Panicum miliare*. The three primary antipodal cells are quite large and highly vacuolate. Often they divide to form 5–6 cells, each containing 1–4 nuclei and are glandular instead of the spear-heading type. No deposit of starch around the egg nucleus or in the antipodal cells was found though recorded by Khosla (1946).

Early divisions of the fertilized egg result in a 4-celled proembryo. The rest of the embryogeny is similar to that of *P. miliare*. Fig. 46 is a vertical section of the mature embryo.

The ovary wall consists of 5–8 or more layers of cells (Fig. 59) instead of only 4–5 as in *P. miliare*. The middle layers collapse and are obliterated. Both integuments disorganize. The protective envelop of the mature caryopsis comprises the two epidermal layers of the pericarp and the strongly suberized nucellar epidermis.



## DISCUSSION

It would be worthwhile to compare the embryology of *Panicum* with that of the rest of the Gramineae investigated so far, to find out differences, if any, in the developmental features. Of the four wall layers of the anther, the tapetum usually consists of binucleate cells. *P. miliare*, however, differs from it in that the cells remain uninucleate throughout development. In this respect it resembles the condition observed in *Pennisetum typhoideum*, a member of the tribe Paniceae (Rangaswami, 1935; Narayanaswami, 1953). Meiosis in pollen mother cells is normal and of the successive type as is also reported in *Panicum variegatum* (Suessenguth, 1919). Supernumerary divisions of either the vegetative or the male nuclei are occasionally observed resulting in the formation of multinucleate pollen grains as in the millets *Sorghum vulgare* (Artschwager and McGuire, 1949), *Pennisetum typhoideum* (Narayanaswami, 1953), and *Eleusine coracana* (author's unpublished observation).

The ovules are bitegmic and crassinucellate although the number of cell layers at the micropylar end does not exceed two. In this respect it differs from that of *Paspalum* and *Sorghum* (author's unpublished work) where it is several cells thick. Also, the growth of the outer integument is arrested so that it does not extend beyond two-thirds of the periphery of the nucellus. Khosla's statement about the outer integument taking part in the formation of the micropyle, is therefore incorrect.

Meiosis in the megaspore mother cell is normal. The chalazal dyad cell always precedes the micropylar cell in division. Tinney (1940) records a similar feature in *Poa pratensis*, i.e., interkinesis in the micropylar cell at a time when the nucleus of the chalazal cell is in the anaphase or in an early prophase in the micropylar cell when the chalazal is in late prophase, or anaphase in the micropylar cell and telophase in the chalazal.

The embryo sac develops as usual. *Panicum miliaceum* differs from *P. miliare* in the possession of an antipodal complex of coenocytic cells. That of *P. miliare* may be of the glandular type as in *Eleusine* and *Echinochloa* (Narayanaswami, unpublished) or spearheading as in *Sorghum vulgare* (Artschwager and McGuire, 1949).

Unlike *Zea mays* (Randolph, 1936) and *Hordeum* (Merry, 1941), where the proembryos have been reported to develop very irregularly and do not conform to any pattern, *Panicum* shows the initial stages (up to 10-12 cells at least) to be very regular. In some cases oblique wall formation in the terminal cell of the proembryo cuts off a central "apical" cell and further divisions are irregular. It is not possible, therefore, to relate the parts of the fully developed embryo to the various sectors of the proembryo as has been done for *Poa annua* (Souéges, 1924).

Organ differentiation of the proembryo conforms to the usual grass type. No epiblast is present and the attachment of the scutellum to the axis is at a short distance from the plumule-sheath, unlike that reported in *Triticum* and *Hordeum* (Merry, 1941). The structure of the mature embryo follows a uniform ground plan as described for *Sorghum vulgare*.

The endosperm is of the free nuclear type and its development

follows the conventional. As starch grains get deposited inside the cells, disorganization of the nuclei occurs. The nucleolus disappears first and the whole nucleus takes a dark stain; then it becomes irregular in shape and eventually develops into a coarse network-like structure. According to Brenchley (1912) the dying off of these nuclei is a direct consequence of the pressure of the accumulated starch grains inside the cell. Gunther (1927) observes that "the nuclei are not only converted into amorphous lumps but are almost dissolved."

The two integuments are obliterated leaving no intercellular space between the suberized nucellar membrane and the pericarp of the mature ovule, unlike that observed in certain specimens of *Zea mays* (Randolph, 1936). However, in other members of the Paniceae like *Paspalum* and *Echinochloa* (author's unpublished work) and *Setaria* (Narayanaswami, 1953, in press) the micropylar portion of the inner integument forming the rim, appears to survive.

A continuous nucellar epidermis of empty cells enclosing the endosperm except on the germinal face of the embryo, is frequently observed even in caryopses of advanced growth. The cells, however, were in a state of collapse and it is possible that only the suberized outer tangential walls forming the so-called nucellar membrane, survives as a protective structure.

Of the pericarp, the inner and the outer epidermal layers alone persist, firmly compressed against each other, although in *Pennisetum* (Narayanaswami, 1953), all cell layers are retained for the most part.

#### SUMMARY

1. The component parts of the individual spikelet have been studied in longitudinal and transverse sections and under maceration. The sterile glumes are essentially similar in structure to the grass leaf. Interspersed among the outer epidermal cells are the cork-silica group, globular and sharp trichomes, and stomata. The fertile lemma and the palea, however, do not possess either the cork or the silica cell. Sclerenchyma cells of different shapes and sizes, and thin and thick-walled parenchyma cells are observed under maceration.

2. The development of the stigmatic papillae has been traced.

3. Microsporogenesis is normal and of the successive type. The tapetal cells remain uninucleate. The pollen grains are three-celled at shedding. These may occasionally show super-numerary nuclei.

4. The stages leading to the formation of the embryo sac are typical. During Meiosis II division in the chalazal dyad cell precedes that in the micropylar one. The embryo sac is organized as usual. The antipodal cells remain undivided and are uninucleate. They are either of the glandular type or spear-heading.

5. Double fertilization occurs. The sequence of cell division in the zygote has been followed and organ differentiation of the proembryo traced. The distribution of the vascular tissue to the differentiating parts of the mature embryo has been studied in longitudinal and cross sections.

6. The endosperm is free nuclear to begin with, later becoming cellular. The peripheral layer functions as a 'cambium'. The nuclei in the mature cells of the endosperm are disorganized.



7. Both integuments are obliterated in the mature caryopsis. Of the nucellus, the suberized nucellar epidermis alone may survive. Even this layer is in a state of collapse. Regarding the fruit wall or pericarp, only the two epidermal layers are retained, the middle layers undergoing disorganization.

8. The embryology of *P. miliaceum* corresponds to that of *P. miliare*. The main points of difference are: (a) the anther tapetum consists of binucleate cells, (b) the outer integument does not take part in the formation of the micropyle as reported by Khosla, (c) a linear row of three cells results from meiosis in megaspore mother cells, (d) an antipodal complex of coenocytic cells is formed, and (e) the number of cell layers in the pericarp is higher than that in *P. miliare*.

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## Effect of Nitrogen Nutrition on Growth and Sporulation of *Alternaria tenuis* Strain B Causing Core Rot of Apples

JAWAND SINGH GREWAL

(Botany Department, Allahabad University, Allahabad, India)

The action of a fungus on a host depends much on its ability to grow and sporulate under suitable conditions. It is, therefore, necessary to study the nutritional requirements of an organism very carefully before one can clearly understand its behavior. *Alternaria tenuis* is parasitic on a number of hosts and it has been observed by Srivastava (14) that the strain of *Alternaria tenuis* which infects wheat grows well on potassium nitrate, d-alanine, d-valine, l-leucine, l-aspartic acid, glutamic acid, asparagine and acetamide. The same fungus was isolated from apples and it was found that this strain of *Alternaria tenuis* differed from the wheat strain in various respects. It has been designated, *A. tenuis* strain B. Mix (10) had also noticed differences in the behavior of *Taphrina caerulescens* isolated from different hosts. He reported that "all species of *Taphrina* showed a characteristic pattern of nitrogen utilization. Some host forms within the species agreed closely in behavior while others showed various degrees of difference." He further found that ammonium chloride was not utilized by *Taphrina caerulescens* from *Quercus macrocarpa* and *Q. prinoides* but the same species isolated from *Q. laurifolia* gave best growth on ammonium chloride. An attempt has, therefore, been made to study the nutritional requirements of *Alternaria tenuis* strain B. The present paper deals only with nitrogen requirements of this particular strain.

### MATERIAL AND METHOD

The strain of *Alternaria tenuis* used in the present investigation was isolated from the core rot of apples. Externally such apples appeared quite healthy. The culture has been maintained on Asthana and Hawker's medium A, containing K NO<sub>3</sub>; 3.5 gms, KH<sub>2</sub>PO<sub>4</sub>; 1.75 gms, Mg SO<sub>4</sub>·7H<sub>2</sub>O; 0.75 gm, glucose; 5 gms., distilled water 1000 c.c. The amount of nitrogen in potassium nitrate of the basal medium was 485 mgs. per litre and for the study of the nitrogen requirement of the fungus this was substituted with equivalent quantity of nitrogen in different organic and inorganic compounds. The amount of peptone added was equal to potassium nitrate.

Liquid cultures containing 50 c.c. of nutrient solution in 150 c.c. conical flasks were sterilized at 10 lb. pressure for 20 minutes. The pH of different media was adjusted to 5.0. Inoculum of equal size was used and the flasks were incubated at 24° C for three weeks. Four replicates were used in each series. The dry weight of the fungus as well as its sporulation were recorded. The mycelial mats were washed with distilled water and filtered through weighed sintered glass crucibles, dried to a constant weight at 80° C. They were cooled in dessicators and quickly weighed in analytical balance. Average results



were calculated. The macroscopic and microscopic characters on different media were carefully recorded. Double distilled water, Pyrex glassware and chemicals of purest available grade were used throughout the experiment. Ridgway's color standards and color nomenclature were used for recording the color of the mycelium. Potassium nitrate of the basal medium was replaced by the following nitrogenous compounds.

*Inorganic compounds*:—ammonium nitrate, ammonium bromide, ammonium sulphate, ammonium chloride, ammonium acetate, ammonium oxalate, ammonium dihydrogen phosphate, ammonium tartrate, potassium nitrate, potassium nitrite, sodium nitrate, sodium nitrite, magnesium nitrate, and calcium nitrate.

*Organic compounds*: glycine, d-alanine, l-leucine, d-valine, l-aspartic acid, glutamic acid, l-asparagine, l-phenyl-alanine, histidine, acetamide methionine, thiourea, urea and peptone.

The color of the mycelium, average dry weight and the nature of sporulation are summarized in Table 1.

TABLE 1. Showing average growth of *Alternaria tenuis* strain B in milligrams and sporulation grade on different nitrogen compounds added to the basal medium at the rate of 485 milligrams of nitrogen per liter.

Nitrogen Source	Average dry wt.	Sporulation	Color of mycelium
Magnesium nitrate	86.9	good	smoky grey
Peptone	86.8	good	drab
d-Alanine	86.6	absent	roods brown
Calcium nitrate	85.4	good	deep grayish olive
Valine	83.3	fair	cinnamon drab
l-Phenyl-alanine	82.6	absent	light cinnamon drab
Ammonium acetate	81.6	poor	mumy brown
Ammonium oxalate	81.1	traces	prouts brown
Glycine	81.1	absent	sorghum brown
Acetamide	77.7	absent	ecru-drab
l-Asparagine	70.4	fair	hair brown
l-Aspartic acid	66.4	good	fuseous black
Glutamic acid	65.4	absent	chaetura black
Urea	60.6	fair	hair brown
Ammonium nitrate	51.1	traces	ochraceous buff
Ammonium tartrate	48.7	poor	ochraceous buff
Potassium nitrate	47.5	good	light drab
Ammonium chloride	47.2	absent	russet
Ammonium dihydrogen phosphate	47.0	traces	pale flesh color
Sodium nitrate	45.1	good	drab grey
Methionine	40.1	absent	gobelin blue
l-Leucine	37.6	absent	deep olive buff
Histidine	37.2	absent	drab
Thiourea	34.4	absent	pale pinkish buff
Ammonium bromide	34.0	absent	light ochraceous buff
Ammonium sulphate	33.6	absent	white
Potassium nitrite	0.0	—	—
Sodium nitrite	0.0	—	—
No-nitrogen	0.0	—	—

General Mean  $\pm$  C.D. at 1% level =  $55.26 \pm 15.03$  = moderate growth.

NOTE:—Traces denotes 1-2 spores in many low power microscopic fields, poor denotes 1-5 spores in a field, fair denotes 6-10 spores per field, good denotes more than 16 spores per field.

The data were analyzed statistically and the average of replicates is given in Table 2.

TABLE 2. *Analysis of Variance* (in mgs)

Sources	D.F.	S.S.	M.S.	F(calc)	Significance
Total	115	85887.07			
Replicates	3	45.82	15.27	.234	No
Treatment	28	80376.55	2870.59	44.125	High
Residuals	84	5464.70	65.056		

Summary of dry weight results and conclusions at 1% level of probability.

Replication	—	non-significant
Treatments	—	highly significant
S.E.	C.D. at 5%	C.D. at 1%
4.033	11.34	15.03

Table 1 indicates that the amount of growth of the fungus on different nitrogen compounds differs considerably. Significantly best growth of the fungus was obtained on magnesium nitrate, calcium nitrate, ammonium acetate, ammonium oxalate, peptone, d-alanine, valine, l-phenyl-alanine, glycine and acetamide. Statistically there was no significant difference in the growth of the fungus on these compounds. Though there was good growth on asparagine, it was significantly less than that on peptone, d-alanine amongst the organic substances and magnesium nitrate amongst the inorganic substances. Moderate growth of the fungus was observed on l-aspartic acid, glutamic acid, urea, ammonium nitrate, ammonium tartrate, potassium nitrate, ammonium chloride, ammonium dihydrogen phosphate and sodium nitrate. Amongst the substances supporting moderate growth, glutamic acid and l-aspartic acid were comparatively better than all the inorganic substances except ammonium nitrate. The growth of *Alternaria tenuis* strain B was significantly poor on methionine l-leucine, histidine, thiourea, ammonium bromide and ammonium sulphate. There was also no statistical difference in the growth of the fungus on these compounds. *Alternaria tenuis* strain B was unable to grow in complete absence of nitrogen or on potassium nitrite and sodium nitrite.

The results of table 1 also indicate that the source of nitrogen in the medium exerts dominating influence on sporulation and color of the mycelium, peptone, l-aspartic acid and all nitrates (except  $\text{NH}_4\text{NO}_3$ ) induced good sporulation. Valine, l-asparagine and urea gave fair sporulation. Poor sporulation appeared on ammonium acetate, ammonium tartrate and only in traces on ammonium oxalate, ammonium nitrate and ammonium dihydrogen phosphate. Contrary



to this ammonium chloride, ammonium bromide, ammonium sulphate, d-alanine, l-phenyl-alanine, glycine, acetamide, glutamic acid, methionine, l-leucine, histidine and thiourea inhibited sporulation and induced the formation of chlamydospores. Ammonium salts in general tried to suppress sporulation.

#### DISCUSSION

The importance of nitrogen in the nutrition of *Alternaria tenuis* strain B was exhibited by the fact that there was no growth when nitrogen was excluded from the nutrient medium. This further showed that the fungus was incapable of utilizing atmospheric nitrogen for its growth. In the present investigation *Alternaria tenuis* strain B failed to grow on potassium nitrite and sodium nitrite. The studies of various investigators (4, 5, 7, 12, 14, 21, 22) showed that nitrites are highly toxic for the growth of certain fungi. Talley & Blank (16), however, did not find any toxicity of nitrite on *Phymatotrichum omnivorum*. Brock (2) working with *Morchella esculenta* and Tandon and Agarwal (18) on *Fusarium coeruleum* found that these organisms could utilize nitrite nitrogen. *Alternaria tenuis* strain B differed from the above fungi because it could not utilize nitrite nitrogen.

Srivastava (14) as well as Uppal et al. (21) found that *Alternaria tenuis* and *Alternaria burnsii*, respectively, gave good growth on potassium nitrate. *A. tenuis* strain B differs from both of them because it gives moderate growth on potassium nitrate. Fergus (3) working on *Penicillium digitatum* found that nitrates (with the exception of  $\text{NH}_4\text{NO}_3$ ) were either not at all utilized or were only poorly utilized. In this respect the present fungus differed from *P. digitatum*. Mix (10) reported that ammonium oxalate gave moderate growth of *Taphrina caerulescens* from *Quercus laurifolia* while its growth was very poor on calcium nitrate and magnesium nitrate (growth was only in traces). These two nitrates gave best growth of *A. tenuis* strain B. Neal et al. (11) also obtained best growth of *Phymatotrichum omnivorum* on calcium nitrate.

Gordon (4) found only fair growth of *Endoconidiophora moniliformis* on ammonium oxalate but it supported good growth of *A. tenuis* strain B. Mix (10) observed that all the twenty seven species of *Taphrina* tried by him were unable to use nitrogen from ammonium acetate. While *A. tenuis* strain B gave good growth on this compound. Neal et al. (11) obtained poor growth of *Phymatotrichum omnivorum* on ammonium nitrate. In the present investigation *A. tenuis* strain B differed from it as it gave moderate growth. Similar results were obtained by others (2, 21) on ammonium nitrate but Lockwood et al. (7) obtained best growth of *Rhizopus oryzae* on it. Mix (10) reported that *Taphrina americana* and *Taphrina caerulescens* from *Quercus macrocarpa* and *Q. prinoides* were unable to use nitrogen from ammonium chloride. Similarly Srivastava (14) obtained poor growth of *Alternaria tenuis* on ammonium chloride. *A. tenuis* strain B, however, differed from them because it gave moderate growth on that substance. Lockwood et al. (7) found that *Rhizopus oryzae* was unable to utilize nitrogen from sodium nitrate but *A. tenuis* strain B was able to use it and gave moderate growth on it. Wolf (24) found that ammonium sulphate

supported good growth of *Ustilago zae* while some other investigators (2, 7, 21) obtained moderate growth of their fungi on it. The present fungus gave poor growth on ammonium sulphate, similar results were obtained by Neal et al. (11) for *Phymatotrichum omnivorum*.

Lockwood et al. (7) and Srivastava (14) found that peptone supported only poor growth of *Rhizopus oryzae* and *Alternaria tenuis*, respectively. The present fungus (*A. tenuis* strain B) differed from them as it gave good growth on peptone. It resembled the fungi studied by Gordon (4) and Tandon (17). In the present investigation l-alanine supported good growth of *A. tenuis* strain B. Similar results were obtained by few other (14, 15, 24) investigators. Lockwood et al. (7), Wolf (23) and Wolf et al. (26) obtained only moderate growth on dl-alanine. Brock (2) obtained poor growth of *Morchella esculenta* on dl-valine, but the present fungus gave good growth and was thus similar to fungi investigated by Srivastava (14) and Wolf (23, 24 and 26). Wolf et al. (26) obtained poor growth of *Monosporium apiospermum* on dl-phenyl-alanine but this compound supported good growth of *A. tenuis* strain B. Similar results were obtained by Srivastava (14) and Wolf (23). Wolf and Shoup (25) observed that all species of *Allomyces* tried by them, were unable to assimilate glycine. *Alternaria tenuis* strain B differed from these fungi and showed good growth. It was thus similar to *Aspergillus niger* and *Monosporium apiospermum* investigated by Steinberg (15) and Wolf et al. (26). Srivastava (14) obtained good growth of *Alternaria tenuis* on acetamide. *A. tenuis* strain B also gave similar results but Brock (2) recorded poor growth of *Morchella esculenta* on acetamide. The present fungus gave good growth on l-asparagine. A number of investigators (4, 12, 14, 24, 27) also obtained similar results for the fungi investigated by them. Srivastava (14) as well as Wolf (23, 24) obtained good growth of *Alternaria tenuis*, *Penicillium chrysogenum*, *Ustilago zae* on l-aspartic acid, and glutamic acid but the present organism differed from them as it gave only moderate growth on those two substances. Though Srivastava (14) obtained poor growth of *Alternaria tenuis* on urea but in the present investigation it supported moderate growth. It is known to support good growth of *Morchella esculenta*, *Endoconidiophora moniliformis* and *Rhizopus oryzae* (2, 4, 7). Mix (10) found that *Taphrina caerulescens* from *Quercus laurifolia* could not utilize nitrogen from dl-leucine and dl-histidine. Wolf (24) observed good growth of *Ustilago zae* on l-leucine and l-histidine. Unlike these *A. tenuis* strain B gave poor growth, and in this respect it was similar to *Morchella esculenta* investigated by Brock (2).

The ability of *Alternaria tenuis* strain B to utilize nitrates and ammonium nitrogen besides organic nitrogen and its failure to use atmospheric nitrogen places this fungus in the third group of Robbins' (13) classification.

Little attention has so far been paid to the role of nitrogen nutrition on the sporulation of fungi. pH of the medium also influences sporulation considerably. Previous investigations by the author showed that this organism sporulates best within a range of pH 4 to 6. The pH of all the media in the present investigation was adjusted to 5.0. *A. tenuis* strain B gave abundant sporulation on peptone, l-aspartic acid,



calcium nitrate, magnesium nitrate, potassium nitrate and sodium nitrate. Mix (9) also found nitrate nitrogen most favorable for the sporulation of many isolates of *Phyllosticta solitaria*. Patel et al. (12), as well as Timnick et al. (20), found potassium nitrate to be a good source of nitrogen for sporulation of *Pestalotia psidii* and *Melanconium fuligineum*. Mathur et al. (8), however, found sodium nitrate a poor and neopeptone an excellent source of nitrogen for sporulation of *Colletotrichum lindemuthianum*. In the present investigation peptone gave good sporulation of *A. tenuis* strain B.

Moderate sporulation of *A. tenuis* strain B was observed on valine, l-asparagine and urea. A number of investigators (1, 6, 12, 19) had reported asparagine to be a favorable source for the sporulation of fungi. Mix (9), however, found that asparagine was a moderate source for the sporulation of *Phyllosticta solitaria*. Similar results were obtained in the present investigation. Mathur et al. (8) had reported asparagine to be a poor and urea an excellent source of nitrogen for the sporulation of *Colletotrichum lindemuthianum*.

Poor sporulation of *A. tenuis* strain B was recorded on ammonium tartrate, ammonium acetate, and only in traces on ammonium oxalate, ammonium nitrate and ammonium dihydrogen phosphate. A number of investigators (6, 12, 20) had reported ammonium tartrate to be a good source of nitrogen for sporulation.

Sporulation of the present fungus was completely checked when ammonium chloride, ammonium bromide, ammonium sulphate, d-alanine, l-phenyl-alanine, glycine, acetamide, glutamic acid, methionine, l-leucine, thiourea and histidine were supplied as a sole source of nitrogen. The ammonium salts checked sporulation and induced formation of chlamydospores. Many investigators (8, 12, 20) found that ammonium sulphate was a poor source of nitrogen for sporulation of fungi investigated by them. Mathur et al. (8) reported that glycine was a poor source of nitrogen for sporulation. Timnick et al. (20) observed that it delayed spore formation of *Melanconium fuligineum* but in the present investigation sporulation was not only delayed but was completely suppressed. Lilly and Barnett (6), however, reported glycine to be a favorable source for the sporulation of *Monilia fructicola*, *Phoma betae*, *Neocosmopara vasinfecta* and *Septoria nodorum* and in this respect those organisms greatly differed from the present fungus. According to Timnick et al. (20) glutamic acid is a favorable source for the sporulation of *Melanconium fuligineum* but *A. tenuis* strain B differs from it as it fails to sporulate on it. It is quite clear from Table 1 that growth and sporulation are not always interrelated. The growth may be good on one substance but sporulation may or may not be good on it. A number of substances supported good growth but on some of them sporulation was distinctly poor or even absent, while on others it was quite good.

#### SUMMARY

The effect of 28 different nitrogen compounds on growth and sporulation of *Alternaria tenuis* strain B causing core rot of apples was determined. The growth was significantly better on magnesium nitrate, calcium nitrate, ammonium acetate, ammonium oxalate,

peptone, d-alanine, l-phenyl-alanine, glycine and acetamide. Many ammonium salts, l-leucine and histidine proved poor sources of nitrogen for the growth of *A. tenuis* strain B. Sodium nitrite and potassium nitrite did not support any growth.

Best sporulation of *A. tenuis* strain B was recorded on peptone, l-aspartic acid and all nitrates (except  $\text{NH}_4\text{NO}_3$ ). Ammonium salts in general tried to suppress sporulation. Fair sporulation was observed on valine, l-asparagine and urea. Spore formation was completely checked on ammonium chloride, ammonium bromide, ammonium sulphate, d-alanine, l-phenyl-alanine, glycine, acetamide, glutamic acid, methionine, l-leucine, histidine and thiourea. There was no correlation between the amount of growth and sporulation.

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## Notes on Fungi of Assam, I.

S. CHOWDHURY

(Department of Agriculture, Assam, Jorhat, India)

Assam, the north-eastern State of India, abounds in dense forests, rivers, dales, and valleys. The climate is temperate with abundant rainfall and high humidity. Vegetation is varied. These topographical features and climatic conditions suggest that this State is likely to possess a rich fungus flora, including many species as yet unrecorded for India and new to science. Unfortunately, so far no exhaustive collections and studies of the fungus flora of Assam have been made. Some collections of fungi in the Khasi Hills were made by Hooker and Thompson early in the nineteenth century and by Butler and Subramanian between the years 1910 and 1915. Bor made some collections of the Polypores of Lokra Hills which were identified and recorded by Bose (1937). An attempt to make an exhaustive collection and systematic study of the fungus flora of Assam was, however, made by the present author (Chowdhury, 1944, 1946 and 1948) who made quite a large collection and recorded a large number of species. The present article is a further contribution on the subject by him based on collections and studies made during recent years.

1. *ASTERINA CAMELLIAE* Syd. and Butl. in *Ann. Myco.* ix: 389, 1911; Saccardo, *Syll. Fung.* xxiv: 474, 1928; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India.* i: 15, 1931.

Appear as black crusts on the leaf; the crust consists of the mycelium and fructifications of the fungus. Perithecia 250–350  $\mu$  in diameter opening when ripe by radiating cracks; asci ellipsoid, 75–100 x 25–35  $\mu$ , each ascus containing 8 ascospores. Ascospores long, elliptical, brown, uniseptate, deeply constricted at the septum, with slightly unequal cells and rounded ends, measure 30–40 x 16–18  $\mu$ .

On leaves of *Thea sinensis* L., Latekujan, 12.i.52, leg. S. Chowdhury.

2. *SPHACELOTHECA CRUENTA* (Kuehn) Potter in *Phytopathology* iii: 98, 1912; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India.* i: 46, 1931; Mundkur and Thirumalachar, *Ustilaginales of India* : 13, 1952.

Syn. *Ustilago cruenta* Kuehn in *Hamburg. Gartenz.* xxviii : 178, 1872; Saccardo, *Syll. Fung.* vii : 455, 1888.

Sori replacing the ovaries, measuring 4–18 x 2–4 mm. and surrounded by a thin, grey membrane; membrane rupturing and flaking away into sterile cells, revealing a dark brown, dusty spore mass surrounding a well-developed columella. Spores olivaceous, spherical or ovoid, slightly irregular, minutely echinulate, 5 to 10  $\mu$  in diameter.

In the ovaries of *Sorghum vulgare* Pers. Haflong. 15.viii.52, leg. S. Chowdhury.

3. *SPHACELOTHECA HYDROPIPERIS* (Schum.) de Bary in *Vergl. Morph. Pilze* : 187, 1884; Saccardo, *Syll. Fung.* vii: 499, 1888; Butler

and Bisby, *Sci. Monogr. Coun. agric. Res. India* i: 47, 1931; Liro, *Die Ustilagineen Finnlands* i: 129, 1922; Sydow, *Ann. mycol.* xxxvi: 437, 1938; Mundkur and Thirumalachar, *Ustilaginales of India* : 15, 1952.

Syn. *Uredo hydropiperis* Schumacher in *Enum. Pl. Saell.* ii : 234, 1803; *Ustilago hydropiperis* (Schum.) Schroeter in *Cohn's Beitr. Biol. Pfl.*, ii : 355, 1877.

Sori ovaricolous; forming ovate bodies, 6–7 mm. long, covered by the floral envelope at the base and a pseudo-membrane dehiscing at the apex, revealing a purple black spore mass and a more or less evident columella. Spores purplish, broadly oblong to oval or spherical, abundantly verruculose, 9 to 18  $\mu$  in diameter.

In the ovaries of *Polygonum hydropiper* L. Shillong, 12.xii.53, leg. S. Chowdhury.

4. *USTILAGO EFFUSA* Sydow in *Ann. myco.* iv: 425, 1906; Saccardo, *Syll. Fung.* xxi: 506, 1912; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India* i: 49, 1931; Pavgi and Mundkur, *Indian Phytopath.* i: 114, 1949; Mundkur and Thirumalachar, *Ustilaginales of India* : 28, 1952.

Follicolous; attacked leaves convolute at first, later unrolling, lower part of sorus hidden under the leaf-sheath; sterile cells hyaline, spherical, verrucose and thick-walled. Spores powdery, mummy brown, spherical, globose to subglobose, 4 to 8  $\mu$  in diameter; epispore dark, thick and echinulate.

On *Arundinella wallichii* Nees at Wahjan. 17.vi.51, leg. S. Chowdhury.

5. *USTILAGO RABENHORSTIANA* Kuehn in *Hedwigia* xv: 4, 1876; Saccardo, *Syll. Fung.* vii: 471, 1888; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India* i: 50, 1931; Pavgi and Mundkur, *Indian Phytopath.* i: 116, 1949; Mundkur and Thirumalachar, *Ustilaginales of India* : 35, 1952.

Sori involving the entire inflorescence, linear-oblong, 5–6 mm. long, at first hidden by the enveloping leaf-sheaths but ultimately visible as a black-brown, dusty spore mass, surrounding the elongate axis of the inflorescence. Spores reddish brown to cinnamon brown, spherical, ovate to broadly oval, occasionally somewhat angled, echinulate, 9 to 14  $\mu$  in diameter; epispore of medium thickness.

In the inflorescence of *Paspalum scrobiculatum* L. Shillong, 5.iv.54, leg. S. Chowdhury.

6. *USTILAGO UTRICULOSA* (Nees) Tulsane in *Ann. Sci. nat., Bot., Ser. 3*, vii: 102, 1874; Saccardo, *Syll. Fung.*, vii: 476, 1888; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India* i: 51, 1931; Pavgi and Mundkur, *Indian Phytopath.* i: 118, 1949; Mundkur and Thirumalachar, *Ustilaginales of India* : 39, 1952.

Syn. *Caeoma utriculosa* Nees in *Syst. Pilze.* i : 14, 1817.

Sori destroying the ovaries and flowers, forming irregular bodies with host tissue, enclosing taupe brown spore mass. Sphores wood brown, spherical to globose, broadly oval, 8 to 10  $\mu$  in diameter; epispore of medium thickness and reticulate.

In the ovaries and other floral parts of *Polygonum orientale* L. Jorhat, 7.iv.53, leg. S. Chowdhury.

7. *PUCCINIA FAGOPYRI* Barclay in *J. Asiatic Soc. Bengal.* lix: 107–08, 1890; *J. Bot.* xxviii: 261, 1890; Saccardo, *Syll. Fung.* ix: 306, 1891; Butler and Bisby, *Sci. Monogr. Coun. agric. Res. India* i: 67, 1931.



Uredospores pale brown, echinulate, oval, measuring  $19-25 \times 14-21 \mu$ . Teleutospores very deciduous, falling off with only a fragment of stalk adhering, dark brown and very variable in size and shape, somewhat constricted at the septum, with a smooth surface and slightly thickened at the apex. A clear nucleolar space is seen in each cell. Fresh spores measure from  $28-36 \times 14-18 \mu$ ; the septum divides the spore into almost equal halves, the upper cell often much broader than the lower and more or less globular. Apical thickening about  $4 \mu$ , the cell wall elsewhere about  $2 \mu$  in thickness.

On the leaves of *Fagopyrum cymosum* Meisson, hypophyllous with circular pale areas on the upper surface of the leaf. Shillong, 7.xi.52, leg. S. Chowdhury. On this host the fungus has been recorded for the first time.

8. *ALTERNARIA SESAMICOLA* Kamamura in *Fungi (Nippon Fungological Soc.)* i: 26, 1931; *Rev. Appl. Mycol.* xi: 350, 1932.

Causing brown spots on the upper surface of leaves. Conidiophores arising singly or in fascicles, simple, erect, more or less flexuose, yellowish brown,  $30-90 \times 3-5 \mu$ . Conidia obclavate, yellowish-brown, produced singly or in chains at the tips of the conidiophores, measure  $25-100 \times 7-15 \mu$  having 3 to 10 transverse and 2 to 6 longitudinal septa.

On living leaves of *Sesamum orientale* L., Titabar, 17.vi.51, leg. S. Chowdhury.

9. *CEPHALOSPORIUM EICHHORNIAE* Padwick in *Mycol. Pap. Comm. myco. Inst.* xvii: 10, 1946.

Buff colored oval spots with dark brown, narrow, annular rings, irregular, 4 to 7 cm. in diameter. Spots covered with mycelial web and conidia of the fungus. Conidia elliptical to short-fusiform,  $4-8 \times 2-2.5 \mu$ , hyaline, formed successively at the tips of erect hyphae and collecting in large groups as false heads.

On living leaves of *Eichhornia crassipes* Solms. Karimganj, 15.xi.52. Leg. S. Chowdhury.

#### 10. *Cercospora adhatodae*, sp. nov. (Fig. 1)

Numerous minute, irregular, almost white spots, 0.5 to 8 mm. in diameter on the upper side of the leaf; often adjacent spots coalesce and larger spots formed. Mycelium both inter- and intra-cellular. Conidiophores produced in clusters and emerge through the stomata or rupturing the epidermis, brown to dark brown in color, being lighter at the tip, straight below and geniculate above, at each geniculation a distinct scar showing the point of attachment of the conidia, measure  $52-188 \times 4-6 \mu$ , usually 0 to 6 septate. Conidia hyaline, acicular, broad at the base and tapering to an acuminate apex, measure  $37-244 \times 3.5-5.5 \mu$ , 2 to 32 septate, with a distinct scar at the base showing the point of attachment to the conidiophore.

On the living leaves of *Adhatoda vasica* Nees, Kokilamukh, 12.ii.51. Collected by S. Chowdhury.

Type specimen deposited in the *Herb. Crypt. Indiae Orient.*, Indian Agricultural Research Institute, New Delhi.

Maculae plurimae, minutae, distinctae, irregulares, fere albae,

0.5–8 mm. diam., in superiore pagina foliorum; saepe maculae adjacentes coalescunt atque formant maculas latiores. Mycelium tum intracellulare, tum intercellulare. Conidiophori aggregati, emergentes per stomata vel epidermidem rumpentes, brunnei ad fusce brunneos colore, pallidiores ad apicem, recti infra, geniculati supra, in unaquaque geniculatione monstrantes cicatricem ubi conidia insiderant, magnit.  $52\text{--}188 \times 4\text{--}6 \mu$  plurimum 0–6 septati. Conidia hyalina, acicularia, lata ad basim, decrescentia in apicem acuminatum,  $37\text{--}244 \times 3.5\text{--}5.5 \mu$ , 2–32 septata, hilo distincto ad basim ornata.

Typus lectus in foliis vivis *Adhatoda vasica* Nees, in loco Kokilamukh, 12.ii.51. leg. S. Chowdhury, et positus in *Herb. Crypt. Indiae Orientalis*, Indian Agricultural Research Institute, New Delhi.

11. *CERCOSPORA CORCHORICA* Petrak and Ciferri in *Ann. myco.* xxx: 310, 1932; Mundkur and Ahmad, *Mycol. Pap. Comm. myco. Inst.* xviii: 10, 1946.

Brown spots on the upper side of the leaf varying in diameter from 1 to 4 mm; often adjacent spots coalesce. Conidiophores arise singly



FIG. 1. Conidia of *Cercospora adhatodae* Chowdhury n. sp.  $\times 480$ .

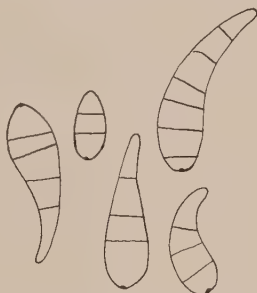


FIG. 2. Conidia of *Helminthosporium litsae* Chowdhury n. sp.  $\times 600$ .

or in fascicles, brown to dark brown in color, measuring  $15\text{--}60 \times 3\text{--}5 \mu$ , 1 to 3 septate. Conidia narrow, more or less cylindrical, olivaceous brown,  $20\text{--}100 \times 3\text{--}6 \mu$ .

On leaves of *Corchorus olitorius* L., Jorhat, 17.viii.54, leg. S. Chowdhury.

12. *CERCOSPORA FAGOPYRI* Muller and Chupp in *Bol. Soc. Venez. Cien. nat.* viii: 35–59, 1942; *Rev. Appl. Mycol.* xxiv: 388, 1945.

Grey green to brown spots, faintly zonate, 1 to 10 mm. in diameter, almost circular in outline on the upper side of the leaf. Conidiophores arise singly or in fascicles, dark brown, multiseptate with 5–6 geniculations,  $50\text{ to }250 \times 4\text{ to }6 \mu$ . Conidia acicular, straight or slightly curved, multiseptate, truncate at the base and tapering at the apex,  $50\text{ to }340 \times 2\text{ to }5 \mu$ .

On leaves of *Fagopyrum cymosum* Meisson. Shillong, 2.vii.54, leg. S. Chowdhury.

13. *COLLECTOTRICHUM CURVATUM* Briant and Martyn in *Trop. Agr.* vi: 259, 1929; Mitra, *Indian J. agric. Sci.* vii: 443–449; 1937.

Brown spots on the upper side of the leaves. Acervuli in abundance on such spots, white or faint pinkish consisting of simple, erect, closely packed conidiophores and setae. Setae brown to dark brown, septate, swollen at the base and tapering towards the tip, formed among the conidiophores and measure  $60-150 \times 4-6 \mu$ . Conidia unicellular, hyaline, falcate and acute at the ends, measuring  $15-24 \times 3-4 \mu$ .

On leaves of *Crotalaria juncea* L. Jorhat, 7.vi.51. leg. S. Chowdhury.

14. *CONIOTHYRIUM ARECAE* Padwick and Merh in *Mycol. Pap. Comm. mycol. Inst.* vii: 4, 1943.

Spots amphigenous, pale green at first, elliptical, up to 5 mm. long later becoming brown; adjacent spots coalesce and eventually the major portion of the leaf is covered. Pycnidia amphigenous  $125-200 \mu$ ; spores dark  $5-7 \times 2.5-4.5 \mu$ .

On living leaves of *Areca catechu* L. Kokilamukh. 1.ix.50. leg. S. Chowdhury.

15. *PHOMA SABDARIFFAE* Sacc. in *Ann. myco.* xi: 554, 1913; Saccardo, *Syll. Fung.* xxv: 105, 1931; Muller and van Eek, *Meded. alg. Proefst. Landb., Batavia* 32, 1939 (*Rev. Appl. Mycol.* xix: 219-221, 1940); Padwick, *Mycol. Pap. Comm. mycol. Inst.* xii: 7, 1945.

Greyish black water-soaked patches appear on the leaf, often the whole leaf area is involved. Pycnidia appear on the older diseased portions of the leaf, gregarious, globose to sub-globose, brown,  $85$  to  $150 \mu$  in diameter. Spores hyaline, fusoid,  $8-15 \times 2.5-4 \mu$ .

On leaves of *Hibiscus sabbdariffa* L. var. *rozella*, Jorhat, 10.ix.51, leg. S. Chowdhury.

16. *PHYLLOSTICTA DIOSCOREAE* Cooke in *Grevillea* viii: 136; Saccardo, *Syll. Fung.* iii: 58, 1884; Da Casta and Mundkur, *Proc. Nat. Inst. Sci. India.* xiv: 58, 1948.

Pale yellow spots on the upper side of the leaf. Pycnidia gregarious, globose to subglobose, brown,  $100-150 \mu$  in diameter. Pycnospores hyaline, ovoid,  $7 \times 5-6 \mu$ .

On leaves of *Dioscorea alata* L. Karimganj, 20.ii.52. leg. S. Chowdhury.

17. *Helminthosporium litsae*, sp. nov. (Fig. 2)

Appear as innumerable minute black velvety masses  $0.5$  to  $3$  mm in diameter over the upper surface of the leaf. These masses consist of the conidiophores and the conidia of the fungus. Mycelium both inter- and intra-cellular. Conidiophores arise in fascicles consisting of a few to many with conspicuous swollen bases, emerging through the stomata or rupturing the epidermis, measure  $86-225 \times 4-7 \mu$ ,  $2$  to  $6$  septate, dark olivaceous in color but lighter towards the tip, with distinct geniculations and conidial scars. Conidia solitary, clavate, straight or slightly curved, olive-brown,  $34-75 \times 7-12 \mu$ ,  $2-7$  septate bearing a distinct hilum at the base.

On the upper side of the living leaves of *Litsaea polyantha* Juss. Gurjgunia, 28.ii.51, collected by S. Chowdhury.



Type specimen deposited in the *Herb. Crypt. Indiae Orient.*, Indian Agricultural Research Institute, New Delhi.

Fungus apparenter constans innumeris acervulis minutis, nigris, 0.5–3 mm. diam., nigris, holosericis, dispersis in totam folii faciem; hi vero acervuli constant conidiophoris atque conidiis fungi. Mycelium tum intercellulare, tum intracellulare. Conidiophori fasciculati pauciores vel plurimi, basi conspicue tumida, emergentes e stomatibus vel epidermidem rumpentes, magnit.  $86\text{--}225 \times 4\text{--}7 \mu$ , 2–6 septati, fusce olivacei colore sed pallidiores ad apicem, geniculationibus distinctis atque cicatricibus conidialibus ornati. Conidia solitaria, clavata, recta vel paulo curvata, olivaceo-brunnea,  $34\text{--}75 \times 7\text{--}12 \mu$ , 2–7 septata, hilo distincto ad basim ornata.

In foliis vivis *Litsaea polyantha* Juss. Typus lectus in loco Gurjgunia, 28.ii.51, leg S. Chowdhury, et positus in *Herb. Crypt. Indiae Orientalis*, Indian Agricultural Research Institute, New Delhi.

The author's thanks are due to Rev. Father Dr. H. Santapau, St. Xavier's College, Bombay for the preparation of the Latin diagnoses of the new species.

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## Studies on Spirostreptoid Millipeds.

### II. The genus *Plusioporus* Silvestri

RICHARD L. HOFFMAN

(Blacksburg, Virginia)

The first generic name to be based upon an American spirostreptoid diplopod was *Plusioporus*, proposed in 1895 by Filippo Silvestri for two South American species which he named *P. salvadorii* and *P. cameranii*. The genus was diagnosed as follows:

"Gen. *Plusioporus*, nov."

"Genus generi *Alloporus* Porat affine—Antennae longae, articulis elongatis—Segmentum primum lateribus non adstrictus, sed latis et sulcatis ut in *Archispirostreptus*—Pori repugnatori a segmento quinto incipientes—♂ Segmenti primi angulus anticus antrorsum valde productus—Pedes copulativi ut in *Archispirostreptus* fere constituti, sed different forma paris postici, quod in *Alloporus* brevi et laminare,<sup>1</sup> in *Plusioporus* perlongum, attenuatum est."

As in the case of many of Silvestri's genera, the diagnostic characters stipulated for *Plusioporus* are not very useful, and the illustrations of the gonopods are very poor (*e. g.*, the telopodite of *salvadorii* is represented by a single, distally forked line). No type species was designated, although a year later (1896) Silvestri did select *salvadorii* for the purpose.

In preparing his paper on the millipeds of the Museu Paulista (1902) Brolemann largely ignored the half-dozen spirostreptoid genera which had been proposed by Silvestri, and no attempt to evaluate the names used for American genera of the Spirostreptidae was made until Pocock undertook the task in the *Biologia Centrali-Americana*. Endeavoring to relate Brolemann's names to Silvestri's earlier ones, he concluded that *Gymnostreptus* is a synonym of *Plusioporus*, *Scaphiostreptus* of *Orthoporus*, and *Cladostreptus* of *Epistreptus*. Of these associations I am now able to concur only with the second instance. The relegation of *Gymnostreptus* to synonymy under *Plusioporus* was founded upon Pocock's misunderstanding of the telopodite of the gonopod of *P. salvadorii* as being "... long, attenuate, and not branched."

Attems' monumental treatise on the spirostreptoids (1914) did nothing to clarify the status of *Plusioporus*. The genus was diagnosed, placed in a generic key next to *Alloporus*, and six species were listed. Of these, only *salvadorii* was correctly placed. One species, very closely related to it, was described in the genus *Scaphiostreptus* (*oyapokanus*).

<sup>1</sup>It should be recalled that Silvestri's concept of *Alloporus* was, in 1895, drawn from his "*Alloporus*" *americanus*, which is not a true *Alloporus* at all, as Silvestri himself later realized.

Most recently, Schubart, in his summary of the Spirostreptidae of Brasil (1945) recognized *Plusioporus* as distinct from most of the other genera on the basis of pore series commencing on the fifth segment. Schubart also described a new species of *Plusioporus* (*cristatus*), which, however, is not congeneric with *salvadorii* and will have to be re-allocated in the classification.

Because of the poor original description, *Plusioporus* has remained something of a *genus inquirendum* to all workers subsequent to Silvestri, who have drawn their concept of the genus from species not isogenotypic with *salvadorii*. Owing to the presence of pores on the fifth segment, it has long been considered by Attems and others to be closely related to the African *Alloporus* (itself still an unsettled entity, having been based upon a female specimen). Obviously, as long as *salvadorii* remained unknown, *Plusioporus* could never be disposed of, and it has been more or less inevitable that a later name would have to be placed in its synonymy. It is a matter of much satisfaction to me to be able to resolve this particular hazard to the stability of spirostreptoid nomenclature. This action is possible because of the fact while Dr. O. F. Cook was working on millipeds, he and Silvestri exchanged a considerable number of paratype specimens, with the result that the U. S. National Museum now contains typical material of *Plusioporus salvadorii*. I am greatly indebted to Dr. E. A. Chapin for the opportunity of studying this valuable material.

Because of the foregoing resumé of the confused history of this group, I have made an attempt to prepare a short treatment of the genus to account for its synonymy and to present a list of the species which appear to the congeneric with *P. salvadorii*. It is hoped that this will be useful to others who may deal with South American spirostreptoids.

#### Genus PLUSIOPORUS Silvestri

- Plusioporus* Silvestri, 1895, Boll. Mus. Torino **10** (203): 10.  
*Alloporus* (not of Porat) Brolemann, 1902, Rev. Mus. Paulista **5**: 143.—Schubart, 1945, An. Acad. Brasileira Sci. **17**: .  
*Nesostreptus* Attems, 1926, in: Kükenthal-Krumbach, Handbuch der Zoologie **4**: 199.—Jeekel, 1952, Entom. Bericht **14**: 74 (type: *Nesostreptus novarae* Attems).  
*Hessonoporus* Attems, 1950, Ann. Mus. Naturh. Wien **57**: 206 (as subgenus of *Alloporus*; type: *A. (H.) carinulatus* Attems).  
*Dicranostreptus* Attems, 1950, Ann. Mus. Naturh. Wien **57**: 220 (as subgenus of *Epistreptus*; type: *Scaphiostreptus oyapokanus* Attems).<sup>2</sup>

*Type*—*Plusioporus salvadorii* Silvestri 1895, by designation of Silvestri 1896.

*Diagnosis*—A spirostreptoid genus in which the pore series commences on the fifth segment; the prefemoral process of the first pair of male legs is large, conspicuous, and nearly quadrate in shape; the distal end of the telocoxite of the gonopods is setose and reaches to approximately the same height as the paragonocoel, the latter without or with but a small angular lateral cone; the telopodite of the gonopods is conspicuously jointed just beyond its exertion, with a rather long acicular process arising proximad of the joint; tarsal element of the

<sup>2</sup>Preoccupied by *Dicranostreptus* Reichenbach 1850 (Aves).



telopodite (beyond joint) rather simple, loosely coiled through one or two circles, usually with a small lateral tooth, tapering distad, seminal channel terminating in a distinct slender solernomerite near the base of which is a characteristic supplementary parsolenomerite process which gives the telopodite the superficial appearance of being distally bifurcate.

*Distribution*—From northern Argentina north through eastern Brasil to French Guiana.

*Synonymy*—*Plusioporus* has recently acquired a rather varied synonymy, most of which is attributable to Count Attems, who, I believe, erred frequently (particularly in his later works) due to a reliance upon

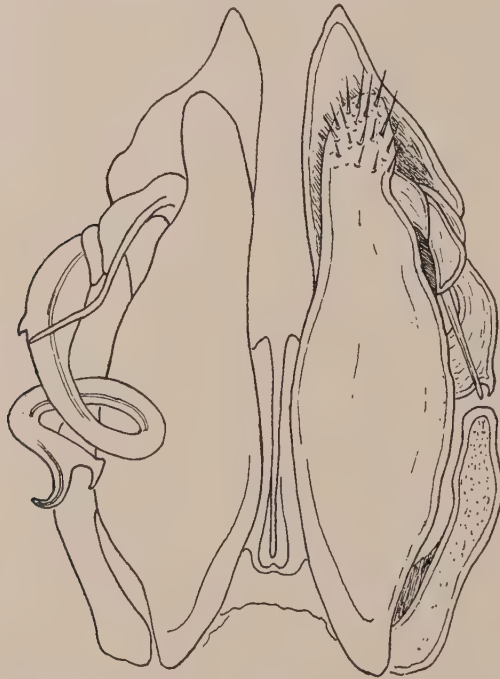


FIG. 1. *Plusioporus salvadorii*, gonopods, anterior aspect (from paratype, U. S. N. M., Resistencia, Chaco, Argentina).

brief verbal characterizations of gonopods rather than on close comparison of drawings or of the appendages themselves. Furthermore, in dealing with the spirostreptoids, he would often distinguish genera on the presence of pores on the fifth segment while elsewhere in the same paper that character would receive only subgeneric value. The same inconsistency obtained, I think, in Attems' interpretation of the term "Tarsalrest". Moreover, Attems did not adhere very closely to the basic concepts and principles of type fixation.

The use of *Alloporus* for a group of South American spirostreptids originated with Silvestri, who somewhat provisionally adopted Porat's

generic name for species from Argentina in which the pore series started on the fifth segment. Although this usage was based solely on the pore character and not on gonopod structure, nearly all subsequent workers have followed Silvestri's precedent. However, in a recent paper (1952), Jeekel has shown conclusively that the Neotropical forms which have gone under the name *Alloporus* are undoubtedly generically distinct from any known African genus, and that in consequence a new name would have to be found for them. This requirement he proceeded to fill by using Attems' name *Nesostreptus*, the type species of which (*novarae* Attems) is congeneric with *setiger* and its several related species. Jeekel also listed the species which he considered congeners of *novarae*, including the French Guianan *oyapokanus* Attems, originally described in *Scaphiostreptus*.

Recently, however, *oyapokanus* was transferred to *Epistreptus* by Attems, obviously in error, and made the type of a new subgenus: *Dicranostreptus*. This unfortunate proceeding resulted in the creation of a junior primary homonym and junior synonym simultaneously, since *Dicranostreptus* is preoccupied and since *oyapokanus* is subjectively congeneric with the type species of an older genus.

At the same time (1950) Attems also observed that the South American species of "*Alloporus*" differed from the African forms, and proposed a new subgeneric name for them: *Hessonoporus* (based upon *carinulatus*, a new species from Brasil). Although Attems' distinction was a good one, he unfortunately did not investigate the likelihood of there being earlier names available for the group.

With continued reference to Attems' 1950 publication, I would call attention to a species described as *Pemptoporus brasiliensis*. Comparison of fig. 52, depicting the gonopods of this species, with fig. 20, (the genitalia of *Hessonoporus carinulatus*) and with the excellent figures of Schubart (1950), leaves no doubt that *brasiliensis* is actually congeneric with *novarae*, *oyapokanus*, *setiger*, and the several species recently described by Schubart. Now the discovery that all of these forms are related to *salvadorii* (as can be readily perceived upon examination of the accompanying drawing) necessitates discontinuing all generic names based upon them in favor of the much earlier *Plusioporus*. It might well be mentioned, in support of a preceeding comment, that Attems separated *Pemptoporus* from *Hessonoporus* in his 1950 treatment in the couplet which follows: "Gonopodentelopodit endwärts immer dünner werdend, im Querschnitt rund, in eine dünne Spitze auslaufend" (leading to *Hessonoporus*) as opposed to "Gonopodentelopodit mehr oder weniger verbreitet" (leading to *Pemptoporus*). But these differences do not show up in the illustrations of the genitalia of *H. carinulatus* and *P. brasiliensis*.

It is true that Attems did recognize the similarity between *brasiliensis* and *novarae*, but placed these two species in *Pemptoporus* (type: *Diaporus augur* Silvestri). I have shown in the preceeding part of this series (Lloydia, 1953, 16: 149) that *augur* is actually congeneric with the type species of *Isoporoastreptus*, of which *Pemptoporus* becomes a junior synonym.

The classification and arrangement of the species within the entire order Spirostreptida is a matter of the greatest imaginable chaos, of

which the preceeding tangle is but a small part. Final resolution will necessitate, unfortunately, a considerable amount of splitting and re-allocation of species from presently heterogeneous genera.

*Species*—I am aware of twelve specific names based upon species of the genus<sup>3</sup>. Of these, some appear to be junior synonyms of others or at best subspecifically distinct. I think it preferable for the time being to list all of these names uncritically, with an indication of their probable status.

**PLUSIOPORUS ARARAQUARENSIS (Schubart)**

*Alloporus araraquarensis* Schubart, 1950, *Dusenia* 1(6): 335, figs. 4, 5.

Type locality—Bueno de Andrade, Mun. de Araraquara, State of Sao Paulo, Brasil.

Range—Known only from the type locality.

**PLUSIOPORUS BRASILIANUS (Attems)**

*Pemptoporus brasilianus* Attems, 1950, *Ann. Naturh. Mus. Wien* 57: 224, figs. 51–53.

Type locality—Brasil, without further data.

Range—Known only from the type specimen.

Comments—A species very close to *setiger* Brolemann, and perhaps a synonym of it.

**PLUSIOPORUS CARINULATUS (Attems)**

*Alloporus (Hessonoporus) carinulatus* Attems, 1950, *Ann. Naturh. Mus. Wien* 57: 206, figs. 19, 20.

Type locality—Bahia, Brasil.

Range—Known only from the type locality.

Comments—Very close to *recifensis*, probably only subspecifically distinct from it. Both species were described in the same year.

**PLUSIOPORUS MARANGUAPENSIS (Schubart)**

*Alloporus maranguapensis* Schubart, 1945, *Rev. Brasil. Biol.* 5(2): 278, fig. 3.

Type locality—Serra de Maranguape, State of Ceara, Brasil.

Range—Known only from the type locality.

Comments—According to Jeekel, this is a synonym of *novarae*.

**PLUSIOPORUS NIGRICOLLIS (Schubart)**

*Alloporus nigricollis* Schubart, 1947, *Bol. Mus. Nac., Zool. Ser.*, 82: 4, figs. 1–3.

Type locality—Leopoldina, State of Mato Grosso, Brasil.

Range—Known only from the type locality.

**PLUSIOPORUS NOVARAE (Attems)**

*Nesostreplus novarae* Attems, 1927, *Arch. Naturgesch.* 92: 251.

Type locality—"Madeira"—doubtless in error.

Range—Probably northeastern Brasil.

Comments—Jeekel (1952) believes that this name is a senior synonym of *A. maranguapensis* Schubart.

<sup>3</sup>Several others, such as *gigliotosi* Silvestri and *cristatus* Schubart, are not true *Plusioporus*.



## PLUSIOPORUS OYAPOKANUS (Attems)

*Scaphiostreptus oyapokanus* Attems, 1914, Zoologica 25 (65/66): 94, figs. 74-77.

*Nesostreptus oyapokanus* Jeekel, 1952, Entom. Bericht 14: 74.

*Epistreptus (Dicranostreptus) oyapokanus* Attems, 1950, Ann. Naturh. Mus. Wien 57: 220.

Type locality—Oyapok, French Guiana.

Range—Known only from the type locality.

Comments—Perhaps subspecifically related to *recifensis*.

## PLUSIOPORUS PANDEIRUS (Schubart)

*Alloporus pandeirus* Schubart, 1950, Dusenía 1(6): 332, figs. 1, 2.

Type locality—Rio dos Pandeiros, State of Minas Gerais, Brasil.

Range—Known only from the type locality.

## PLUSIOPORUS RECIFENSIS (Schubart)

*Alloporus recifensis* Schubart, 1950, Dusenía 1(6): 333, fig. 5.

Type locality—Recife, Afogados, State of Pernambuco, Brasil.

Range—Known only from the type locality.

## PLUSIOPORUS SALVADORII Silvestri

*Plusioporos salvadorii* Silvestri, 1895, Boll. Mus. Torino 10 (203): 10, fig. 10.

Type locality—Resistencia, Territory of Chaco, Argentina.

Range—Northern Argentina and adjacent Paraguay.

## PLUSIOPORUS SETIGER (Brolemann)

*Spirostreptus (Alloporus) setiger* Brolemann, 1902, Rev. Mus. Paulista 5: 146, figs. 170-78.

*Alloporus (Hessonoporus) setiger* Attems, 1950, Ann. Naturh. Mus. Wien 57: 206.

Type locality—Alto da Serra, State of Sao Paulo, Brasil.

Range—Sao Paulo and adjacent parts of Pirassununga, Brasil.

Comments—The illustration of the gonopod of this species given by Schubart (1944) is somewhat different from Brolemann's original drawing, and probably reflects the possibility that *setiger* is a polytypic species.

## PLUSIOPORUS SICKI (Schubart)

*Alloporus sicki* Schubart, 1950, Dusenía 1(6): 337, figs. 6, 7.

Type locality—Xavantina, Rio das Mortes, State of Mato Grosso, Brasil.

Range—Known only from the type locality.

Another species has traditionally been associated with these forms since its description in 1902. This is *Alloporus princeps* Brolemann. Despite the considerable body of precedence in this matter, I do not think *princeps* is a congener of any of the preceding species, an opinion shared by Jeekel (1952) who notes that "... it may belong in the neighbourhood of *Conchostreptus*."

The remaining species, it would appear, may be divided into two groups based upon the configuration of the telocoxite of the male gonopod. This distinction has already been perceived by Schubart, who utilized it in a key to the Brazilian species of this genus which

he published in 1950. In one group, including *araraquarensis*, *brasilianus*, *nigricollis*, and *setiger*, the distal part of the telocoxite has a definite triangular lateral lobe. The other group, embracing *sicki*, *salvadori*, *pandeirus*, *recifensis*, *carinulatus*, *oyapokanus*, *maranguapensis*, and *novarae*, has the outer side of the telocoxite merely obliquely slanted, without a separate process. The supplementary character used by Schubart, the presence or absence of a dentiform projection on the inner margin of the telocoxite, is not infallably correlated with the shape of the outer distal margin, as the projection is absent in both *salvadorii* and *sicki*, which are in other respects referable to the group in which it is present.

The "Setiger Group" numbers four species, one of which (*nigricollis*) is quite distinct, while the others are rather closely related in gonopod structure and may be shown to be geographic races of *setiger*. Of the "Salvadorii Group", *pandeirus*, *sicki*, and *salvadorii* appear to be discrete species, with the other five being members of a single species-complex.

The discovery of numerous additional forms, particularly in central eastern Brasil, is to be expected.

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## Observations on the Sexual Behavior of Captive Turtles

JOHN M. LEGLER

(*Museum of Natural History, University of Kansas, Lawrence, Kansas*)

Sexual behavior in the snapping turtle (*Chelydra serpentina*) and the soft-shelled turtles (*Trionyx*) was observed in a group of individuals kept in captivity. Little has been reported heretofore concerning the sexual behavior of these turtles, although excellent and detailed information is available on the sexual behavior of certain other turtles, including the genera *Chrysemys*, *Pseudemys*, *Emys*, *Terrapene*, *Testudo*, and *Gopherus*.

Captive turtles were observed in each of two identical tanks at the University of Kansas. These tanks were 48½ inches deep, 78 inches long, 36½ inches wide at the top, and 13 inches wide at the bottom. One side of each tank consisted of plate glass which was nearly flush with the wall of the tank room, the other side (*i.e.*, that side farthest from the observer) sloped backward from the narrow bottom. The tanks were brightly lighted from above on one side of the wall enabling the observer to sit in the dark on the other side and clearly observe any activity within. During the course of these observations the tanks were drained and cleaned at irregular intervals. Turtles were fed with laboratory mice.

### CHELYDRA SERPENTINA

Six *Chelydra serpentina* were taken from a mud flat five and one half miles northwest of Lawrence, Douglas County, Kansas, where they were hibernating on November 22, 1953, and were placed in one of the tanks. The next day the tank was cleaned and refilled with water. Sexual activity was observed first on November 25 and was observed almost daily thereafter until June, 1954 (when the investigation was terminated), except during periods when the tank was again drained and refilled. Cessation of sexual activity during periods of draining and refilling was probably due to lowering of the water temperature. Water coming from the tap above the tank was approximately 14° C and, after standing in the tank for several days, reached a temperature of approximately 25° C. The temperature of the tank room ranged from 25–29° C. The intensity of sexual activity seemingly was not correlated with the amount of food available since turtles mated as often during periods of starvation as they did after a heavy meal of mice.

Precoital behavior varied; males often directly approached females on the bottom of the tank and mounted them at once. In each of several matings a male followed a female about the tank for a few minutes and then mounted her at or near the surface. The pair would then sink slowly to the bottom. Once I observed a pair facing each other on the bottom with necks extended and noses about one inch apart. Both turtles were so situated that the anterior edge of the plastron touched the bottom and the hindquarters were elevated to



the maximum by downward extension of the hind legs, a posture resembling that of an angry individual preparing to strike. The turtles executed sudden sideward sweeps of the head and neck, simultaneously and in opposite directions, subsequently bringing the neck slowly back so that it was parallel to the midline of the body. This action was repeated about ten times at intervals of approximately ten seconds. No further sex play took place in the following half hour. It was impossible to see whether or not the turtles were forcing water out of the nostrils although they did open and close their mouths at irregular intervals. Taylor (1933: 271), on one occasion, found a pair of snappers in copulation but did not describe their behavior. Concerning another incident, Taylor (*loc. cit.*) states, "Two *Chelydra serpentina* were seen on November 11, their heads close together in shallow water; they appeared to be gulping in water and then forcing it through their nostrils, causing a 'boiling' of the water in two areas above their heads at the surface." Taylor was not certain that this behavior constituted courtship activity.

In the coital position the male is astride the carapace of the female, gripping the edges firmly with the toes and claws of his fore- and hind-feet. Conant (1938: 128) observed the mating of captive snappers on several occasions. The male mounted the carapace of the female, which he grasped with all four feet, and curled his tail under her, at the same time extending his chin over her snout and making it impossible for her to extend her neck. Reciprocal biting of forelegs was observed and males were seen mounting other males.

The exact position of the male upon the female varies according to their relative sizes. A male equal in size to the female will bring the center of his plastron over the approximate center of her carapace. A male smaller than the female mounts the carapace in a more posterior position. In mounting, the male may approach the female from almost any direction and often clasps her firmly when the positions of the two are reversed, end for end, or when the midlines of their bodies are at varying angles to each other. When this occurs, the male may release the female, but more often he maneuvers himself into the coital position by shifting all four feet along the edge of the female's carapace, the relative positions of his feet remaining almost unchanged. Claspings by the male may be, in part, a response to tactile stimulation of the plastron and legs. A male would often mount and clasp another male snapping turtle, or a turtle of another species which happened to touch his legs or the bottom of his plastron. On several occasions the writer observed a male mounting another male who was already clasping a female, thereby forming a "stack" of three turtles with the female on the bottom and the two males on top.

As the male secures a firm grip on the female and gains the coital position, two actions occur simultaneously: the tail is looped under and partly around the tail of the female to bring the anal openings into contact; and the neck of the male is fully extended with the head cocked at an angle of about 45° and held over the head of the female. This action usually causes her to retract her neck somewhat and to hold it in this withdrawn position. The angle of the male's head is accentuated by the supraoccipital process of the skull, causing the

overlying skin and muscle to protrude on the dorsal surface of the neck. The female may elevate her tail and this probably facilitates anal contact and intromission.

When a pair of turtles is in the coital position already described, the male, with neck extended and tail in the proper place, begins a series of violent, co-ordinated, muscular contractions. These contractions involve all four legs, the neck, and the tail. The neck is thrust forward and downward. The male may bite the female about the head and neck, sometimes retaining a hold on a fold of loose skin, but probably not injuring her. Flexures of the tail elevate the tail of the female and improve anal contact. The flexing of the legs tends to pull the male closer to the female but does not involve pounding of her carapace, as Taylor (*loc. cit.*) described for *Kinosternon flavescens*, since the male always remains in fairly close contact with the female. Each spasm of muscular contraction produces a considerable jolt which is reflected upon the bodies of both male and female, particularly upon the fleshy legs of the male which quiver much in the manner of jelly on a plate. Muscular spasms occur before, during, and after intromission, and possibly facilitate penetration of the female cloaca by the penis of the male.

Intromission was assumed to occur when the anal openings were in direct contact. Only occasionally, when the anal contact was broken by a sudden movement of either sex, was the penis visible, and then it was promptly retracted until anal contact was re-established. On one occasion a male resting alone on the bottom had his hindquarters elevated, tail flexed ventrally, and penis extruded. A white discharge issued from the penis. Shortly afterward this male mated with a female nearby. Evans (1953: 192) describes a similar occurrence for *Terrapene c. carolina*.

On one occasion a male *Chrysemys picta bellii* swam up and nudged the tails of a copulating pair of snapping turtles. The male snapper withdrew from the female and before he could retract his penis the painted turtle bit it three times. The anal opening of one male which died in captivity was found to be badly mutilated and a dissection revealed that part of the penis had been torn away. Wood (1953: 185-186) reports triggerfish, *Balistes carolinensis*, biting at the penis of a captive male loggerhead turtle, *Caretta c. caretta*.

The role of the female in mating is chiefly passive although at times she may struggle violently and retaliate as the male bites her, forcing her to retract her head and neck. In one instance, when the buoyancy of the female caused her forequarters to rise, thereby unbalancing the clasping male, he reversed his position in the manner previously described and, with his weight thus redistributed, brought the plastron of the female to rest upon the bottom once more. In one mating, where a female's struggles were especially violent at first, the male retained his hold on her for nearly an hour. After about 15 minutes she ceased her struggles and rotated slowly, finally coming to rest on her back. The male retained his grip during this procedure without altering his position so that the pair was finally resting plastron-to-plastron. Intromission was accomplished several times in this position. When the male released his grip and swam away, the female remained



on her back for approximately five minutes; then she turned over and tried repeatedly and unsuccessfully to reach the surface. After another half hour her movements became unco-ordinated and she appeared to be in acute discomfort. At this time I brought her to the surface with a blunt hook where she floated for several days before dying.

The male generally released the female and swam away after a mating period of from five minutes to one hour. Occasionally the male would retain his hold for a time and continue the spasmodic muscular contractions without attempting intromission. Usually both male and female surfaced for air soon after coitus.

McCauley (1945: 149) describes a fight between two large males which may have been related to some sort of sexual activity. The turtles under my observation never engaged in combat except when the tank was drained. At this time they would snap viciously at anything that moved and would continue to do so until the water again reached a level of two or three feet.

#### TRIONYX

Conant (1938: 160) twice saw pairs of *T. ferox spinifera* in the field in positions suggestive of mating activity. He stated that, "The male had its forefeet placed upon the back of the female in such a way that his hindfeet were beyond the posterior border of her shell and his tail could be turned so that its ventral surface met hers." Conant did not definitely observe copulation. Mitsukuri (1905: 263) stated, that in *T. japonicus*, "Copulation takes place on the surface of the water in the spring."

In the autumn of 1953, two females to *T. mutica* (both approximately 230 mm. in carapace length) were placed in one of the tanks at the University of Kansas. In the spring of 1954 a male *T. ferox hartwegi*, approximately 180 mm. in carapace length, was placed in the same tank with these females. On the afternoon of March 30, the male was actively courting one of the *T. mutica* females. The male swam around and over the female, often approaching her from the rear and then stopping suddenly and hovering over her. When the male was in this position I thought I could detect movements of his forefeet against the anterior part of the female; these movements were vaguely suggestive of the forelimb vibrations seen in mating *Chrysemys* and *Pseudemys*. These movements may have been the result of the male backing water with his forefeet to stay over the female. As the turtles continued their movements about the tank they frequently surfaced to breathe. The female periodically dived to the bottom of the tank and nervously rooted in the gravel there with her snout and forefeet until the male again approached her, at which time the chase about the tank would be resumed. The male generally followed the female but occasionally she would turn suddenly and begin to follow him. At times the male nipped at the anterior part of the female's carapace. During the entire period of courting, the posterior flap of the female's carapace was turned slightly up while that of the male was turned down.

Several times the female sank to the bottom and remained motionless. The male would then approach her from the rear, crawl upon her carapace, and immediately thrust his tail beneath it. The male did



not appear to clasp the female with his feet. The anal openings were brought into contact and intromission probably occurred but this could not be definitely determined. The male remained in the coital position for approximately 15 seconds and then began to drift to one side, slowly rotating the long axis of his body  $180^\circ$  until he faced away from the female and began to swim away. Both turtles would then become active again and the entire procedure, probably ending in coitus, would be repeated. Five unions of this type occurred in one half hour.

The same basic pattern of mating behavior was observed on other occasions throughout the spring of 1954. I am aware that observations of this type are of doubtful validity when made under laboratory conditions. My observations indicate, however, that the courtship patterns of *T. mutica* and *T. ferox hartwegi* are not dissimilar and, that in areas where both species occur, reciprocal matings are possible.

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